

A REVISION OF THE GENUS
HIPPOSIDEROS



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A REVISION OF THE GENUS *HIPPOSIDEROS*

By J. E. HILL

SYNOPSIS

A taxonomic revision of the Microchiropteran genus *Hipposideros* is presented in this study which is primarily devoted to an examination of the genus at the specific and higher levels, with marked emphasis on the detailed diagnosis of its numerous species, their relationships, supraspecific groupings and probable phylogeny.

INTRODUCTION

THIS revision is based on the unequalled collections of the British Museum (Natural History), which contain an extensive series of the genus *Hipposideros*, complemented by a wealth of type specimens, and is principally concerned with the classification of the genus at the specific and higher levels. Detailed monographic treatment at the subspecific level would entail larger series than are at present available for many subspecies and to avoid uneven treatment of the genus has not been undertaken, although wherever possible some note has been taken of subspecific variation. Attention has been directed explicitly to the determination of the relationships between the species and species groups of this large genus and for this purpose detailed study has been concentrated at the level of the species. The results of this study are presented in the form of diagnoses of the numerous species included within *Hipposideros*, often based on the original material, in many cases supported by a further series of specimens, and of the species groups into which the genus can be divided. It has been possible to determine relationships between species, especially among those hitherto inadequately described or poorly known and to determine the validity and extent of the supraspecific groupings within the genus. The subsequent study of these groupings and their relationships has suggested a classification of *Hipposideros* and has given some indication of phylogeny within the genus. All measurements are in millimetres : forearm lengths are given in the form of histograms in the text, while minima, maxima and means (in parentheses) of representative cranial dimensions appear in a terminal table.

Genus *HIPPOSIDEROS* Gray, 1831

Hipposideros Gray, 1831 : 37. Type species by subsequent designation (Sclater (1901 : 116)) *Vespertilio speoris* Schneider.

Hipposiderus Gray, 1834 : 53. Emendation.

Phyllorrhina Bonaparte, 1837 : fascicule 21 (sub. *Rhinolophus ferrum-equinum*). Type species by subsequent designation (Sclater (1901 : 116)) *Rhinolophus diadema* Geoffroy.

Macronycteris Gray, 1866a : 82. Type species by monotypy *Rhinolophus gigas* Wagner.

Gloionycteris Gray, 1866a : 82. Type species by monotypy *Rhinolophus armiger* Hodgson.

Rhinophylla Gray, 1866a : 82. Type species by monotypy *Phyllorrhina labuanensis* Tomes.

Preoccupied by *Rhinophylla* Peters (1865a : 355, 1865b : 520), a genus of Phyllostomatidae. *Speorifera* Gray, 1866a : 82. Type species by monotypy *Hipposideros vulgaris* Blyth = *Rhinolophus larvatus* Horsfield.

Chrysonycteris Gray, 1866a : 82. Type species by monotypy *Hipposideros fulvus* Gray.

Doryrhina Peters, 1871a : 324. Type species by monotypy *Phyllorhina cyclops* Temminck.

Sideroderma Peters, 1871a : 324. Type species by monotypy *Phyllorhina fuliginosa* Temminck.

Ptychorhina Peters, 1871a : 325. Type species by monotypy *Rhinolophus caffer* Sundevall.

Cyclorhina Peters, 1871a : 326. Type species by subsequent designation (Tate (1941 : 354))

Phyllorhina obscura Peters.

Thyreorhina Peters, 1871a : 327. Type species by monotypy *Phyllorhina coronata* Peters.

Syndesmotis Peters, 1871a : 329. Type species by monotypy *Phyllorhina megalotis* Heuglin.

Hipposiderus Blanford, 1888 : 637. Emendation.

Taxonomic history of the genus

The early generic history of *Hipposideros* is confused and the availability of the names employed for the genus has been discussed by Blanford (1888 : 637), Palmer (1904 : 327, 535) and Oey & Feen (1958 : 226). The first generic name to be applied exclusively to a horseshoe bat was *Rhinolophus* Lacépède, 1799, and this name, for type species *Vespertilio ferrum-equinum* Schreber, 1774, the European greater horseshoe bat, was gradually brought into general use for all species of horseshoe bat as each was discovered and made known to science. Later, Leach (1816 : 5) introduced *Phyllorhina* for type species (by monotypy) *Vespertilio minutus* Montagu, 1808, the lesser horseshoe bat of Great Britain and Ireland, listing a specimen presented to the British Museum by G. Montagu with the citation :

Phyllorhina minuta

Small Leafnose

Torquay, Devon.

G. Montagu, Esq.

This citation follows that for *Rhinolophus ferrum-equinum*. The combination *Phyllorhina minuta* employed by Leach is listed by Miller (1912 : 149) and Ellerman & Morrison-Scott (1951 : 115) as a nomen nudum and as a possible synonym of *Rhinolophus hipposideros hipposideros* (Bechstein), 1800. However, Leach has clearly applied a new generic name to the species described by Montagu, now called *Rhinolophus hipposideros minutus*. Oey & Feen (1958 : 226) state that Leach employed *Phyllorhina* as a subgeneric name within *Rhinolophus* for the lesser horseshoe bat from England, retaining the greater horseshoe bat within the nominate subgenus. Leach, however, used both names in the generic sense, calling the greater horseshoe bat *Rhinolophus ferrum-equinum* and the lesser horseshoe bat *Phyllorhina minuta*. As Oey & Feen point out, no subsequent author has arranged *Rhinolophus ferrum-equinum* and *Rhinolophus hipposideros* (of which *Vespertilio minutus* Montagu, 1808 is now considered to be the British subspecies) under different genera or subgenera. *Phyllorhina* Leach, 1816, must therefore be considered a junior synonym of *Rhinolophus* Lacépède, 1799.

Gray (1831 : 37) first recognized the characteristic distinctions of the hipposiderine noseleaf, and with a valid diagnosis proposed the generic name *Hipposideros* for a number of Asiatic species hitherto referred to *Rhinolophus*. Sclater (1901 : 116) designated *Vespertilio speoris* Schneider as its type species. In a later work, Gray (1834 : 53) referred to this genus, using the amended spelling *Hipposiderus*. Peters (1871a : 312) and Dobson (1876 : 58, 1878 : 127) have quoted this name and reference in their synonymies of the genus and were apparently unaware of the earlier citation as *Hipposideros*. Later, Gray (1838 : 492) reverted to the original spelling and provided a further brief diagnosis. *Hipposideros* Gray, 1831, however, did not gain general acceptance and a number of authors, including Peters (1871a : 312) and Dobson (1876 : 58, 1878 : 127) employed *Phyllorrhina* Bonaparte, 1831, often rendering the name as *Phyllorhina*. This name is generally cited from C. L. Bonaparte, 1831, Saggio di una distribuzione metodica degli Animali Vertebrati. Two versions of this work exist in the Library of the British Museum (Natural History). It was published in two sections, the first concerned principally with the homoiothermic animals and the second the poikilothermic animals. The second section includes a further part giving additions and corrections to the first section. The first publication of this work is apparently in an Italian journal, Giornale Arcadico di Scienze, Lettere ed Arti, published quarterly in Rome. The first section appears in the issue for January, February and March, 1831, tome 49, part 1, pp. 3-77, the part number referring only to the number of issue for any one year and appearing only on the binding. The second section appears in the issue for October, November and December, 1831, tome 52, part 4, pp. 129-209. In this version of the work the name (spelt *Phyllorrhina*) appears on p. 15 as follows, 40 referring to its position in the table of genera and 16 to the number of species the genus includes :

- | | | |
|----------------------------------|------------------|-----|
| 40. <i>Rhinolophus</i> , Geoffr. | Eur. As. Af. Oc. | 16. |
| 1. <i>Rhinolophus</i> , Leach | | |
| 2. <i>Phyllorrhina</i> , Leach | | |

The second version of this work in the Library of the British Museum (Natural History) consists of two separately bound sections, corresponding to the two sections of the work as published in the Giornale Arcadico. The first section is almost identical with that in the Giornale Arcadico, but has a title page, the heading Scienze omitted and has been separately paginated. It is dated 1831 and was printed by Antonio Boulzaler, the printer of the Giornale Arcadico. The entry quoted above appears on p. 16 of this version of the work, and this apparently is the version quoted by Peters (1871a : 312), Dobson (1876 : 58, 1878 : 127), Blanford (1888 : 637), Palmer (1904 : 535), Sherborn (1929 : 4932) and Oey & Feen (1958 : 226) who without exception cite the name as *Phyllorrhina*. The second section of the work has been similarly treated in the second version, with the addition of a title page, the omission of the heading Scienze and with separate pagination, but is dated 1832, suggesting that this separately bound version, quoted by authors, is but a reprint of the version printed in the Giornale Arcadico. It is not clear from the citation whether Bonaparte in this work employed *Phyllorrhina* as a subgenus

of *Rhinolophus* in the sense of its generic usage by Leach (1816 : 5) or in the sense of *Hipposideros* as proposed by Gray (1831 : 37). In any case, the absence of diagnosis or of type species invalidates its proposal as a new name, as recognized by Palmer (1904 : 535), Sherborn (1929 : 4932) and Oey & Feen (1958 : 226).

Bonaparte (1837 : fascicule 21) under *Rhinolophus ferrum-equinum*, revived *Phyllorrhina* as a subgeneric name for the first section of *Rhinolophus* as listed by Temminck (1835 : 1-24), corresponding to the genus *Phyllorrhina* of subsequent authors. Bonaparte gives a brief diagnosis and Sclater (1901 : 116) has designated *Rhinolophus diadema* Geoffroy as its type species. It was subsequently raised to generic rank by Peters (1852 : 31) who cited it, however, from Bonaparte (1831). Blanford (1888 : 637) rejected *Phyllorrhina* Bonaparte, 1837 on the grounds that *Hipposideros* Gray, 1831 had priority and that the name, which he rendered as *Phyllorrhina*, had been originally proposed by Leach for a species of *Rhinolophus* and could not therefore be used for another genus. Palmer (1904 : 535) and Sherborn (1929 : 4932) reject it on ground of homonymy with *Phyllorrhina* Leach, 1816, although both correctly citing the name as *Phyllorrhina*. Oey & Feen (1958 : 226) reject the name since at that time the alteration in spelling was considered insufficient under the International Code of Zoological Nomenclature to revive an unavailable generic name. However, Article 56(a) of the International Code of Zoological Nomenclature, 1961 states explicitly that two genus-group names are not to be considered homonyms even if the difference between them is due only to one letter, although it is recommended (Appendix D.3) that the proposal of such names should be avoided. Under these circumstances, therefore, *Phyllorrhina* Bonaparte, 1837, cannot be held to be a homonym of *Phyllorrhina* Leach, 1816, and must be regarded as available within *Hipposideros* if subgeneric division of that genus is required.

Earlier students of the genus or of parts of it include Temminck (1835), Gray (1838, 1866a), Peters (1871a), Dobson (1876, 1878), Andersen (1905, 1906a, 1906b, 1918), Tate (1941) and Aellen (1952, 1956a, 1956b). Gray (1831) originally associated seven Asiatic species with the genus *Hipposideros*. Temminck (1835) reviewed the genus *Rhinolophus* in some detail, but made no formal recognition of the separation of that genus introduced by Gray. This author instead separated *Rhinolophus* into two sections, the first of these corresponding to *Hipposideros* of Gray (1831) or to *Phyllorrhina* of later authors such as Peters (1871a) and Dobson (1876, 1878), adding a number of species to those attributed to *Hipposideros* by Gray and including an African species for the first time. Gray (1838) gave a brief review of *Hipposideros* and added a number of Asiatic species to the genus as listed by Temminck. Later, Gray (1866a) proposed six new generic names for species hitherto referred to *Hipposideros*. Peters (1871a) reduced these to subgenera and proposed six further subgeneric names. This work, the first critical study of the genus, thus greatly divided it but at the same time grouped under numerous subgeneric names the many species and their synonyms that had accumulated since Temminck and Gray first studied the genus as a whole. Gray (1866a) and Peters (1871a) were principally concerned with the diagnosis of the species groups into

which *Hipposideros* is divisible, and although no great use has been made by other authors of subgenera within the genus, their subgenera in a number of cases have been recognized as species groups by most subsequent authors. Dobson (1876, 1878) placed the names proposed by Gray in the synonymy of *Phyllorhina* (= *Hipposideros*) and did not mention the subgeneric groupings of Peters, but at the specific level greatly amplified the revisionary work begun by Peters and provided detailed descriptions of the ears and noseleaves of individual species.

Andersen (1905, 1906a, 1906b) began the first modern detailed revisionary work on the genus with studies of the *diadema*, *armiger*, *commersoni* and *caffer* groups, and in Andersen (1918) Oldfield Thomas published on his behalf a compilation of diagnostic characters presented in the form of keys to the species and subspecies of some of the groups of *Hipposideros*, including brief diagnoses of a number of new forms. This work was probably an extract from a detailed revision upon which Andersen was working at the time of his disappearance and which was never completed. Tate (1941) in a comprehensive review of much of the genus greatly amplified the work of Gray, Peters and Andersen in the definition and diagnosis of its major groups, retaining for the most part the divisions originally proposed by Gray and Peters and allocating to them the species and subspecies more recently proposed. Tate, however, was primarily concerned with the Asiatic species of the genus and made no detailed survey of its African representatives, touching only briefly on their relationships to their Asiatic congeners. His work is nevertheless the only extensive survey of the genus since it was studied by Peters (1871a) and Dobson (1876, 1878) and has provided an excellent basis for its further revision. Although subsequent authors, notably Aellen (1952, 1956a, 1956b), have made valuable contributions to our knowledge of *Hipposideros*, especially to that of its African members, no student since Peters (1871a) and Dobson (1876, 1878) has attempted revisionary study of the genus as a whole, and it now stands badly in need of synthetic study.

Morphological criteria in the genus

The external features of the genus *Hipposideros* have been described by Dobson (1878 : 127) and the principal features of its skull by Miller (1907 : 111), while Tate (1941 : 357) has reviewed the major diagnostic criteria of importance within the genus. As might be expected of so large a genus, it displays a wide range of variation both externally and cranially. The ears, exceptionally united at the base by a low band of integument, vary in outline from comparatively short, broad and rounded or bluntly pointed to long, narrow and with an acute point. Their anterior or inner edge is generally convex, their posterior or outer edge straight or with a shallow concavity or emargination just behind the tip. Some species exhibit a well-defined internal fold at the antitragal lobe, in others absent or represented by a thickening of the membrane of the ear at this point. The external surface of the ear is usually naked except at its base but in some species can be covered with body fur for one half to two thirds the length of the ear. The nasal foliations are complex and consist basically of three sections, in this paper described as the anterior,

intermediate and posterior noseleaves. The noseleaf in many species is flanked by one or more lateral supplementary leaflets, of which in some cases one may extend anteriorly beneath the anterior leaf on to the upper lip, sometimes forming a complete supplementary leaflet encircling the muzzle beneath the anterior leaf. The anterior noseleaf, extending over the upper lip, is the horseshoe of earlier authors, and is rarely much modified but occasionally displays a narrow median emargination. The nostrils open in paired depressions in the centre of this leaf, the narial openings separated by an internarial septum which is usually narrow or only slightly inflated but which may be bulbous, inflated or specialized to form a disc-like structure between the nostrils. Lateral narial lappets project from the outer walls of the narial depressions and together with the internarial septum may become modified to form deep pockets in which lie the narial apertures. The intermediate part of the noseleaf lies immediately behind the narial depressions, forming their posterior boundary, and is a cushion-like structure extending transversely across the entire noseleaf. It may be variously modified by the development of raised median and lateral eminences or ridges, or of a median club-like structure. Its posterior margin forms the base of the posterior leaf, an erect structure with a smooth or sometimes slightly lobulated upper edge, usually convex in outline but on occasion slightly triangular or specialized by the development of a median projection. The anterior face of the posterior leaf is more or less concave, the concavity smooth or divided by one or more vertical septa, enclosing small cells or pockets. The posterior face is usually smooth but in some species is modified by the development of a transverse supplementary structure with a serrated upper edge. The nasal foliations exhibit an exceptionally wide range of variation within the genus from small, comparatively simple structures showing little or no evidence of specialization to large, greatly modified structures completely covering the entire muzzle. A frontal sac, usually less developed in female specimens than in male, with its opening behind the posterior noseleaf, is to be found in a number of species, while a few species are noted for the development, especially in males, of transverse fleshy lobate prominences on each side of the opening of this sac.

The skull demonstrates a similarly wide range of variation, especially in the rostral, palatal and sphenoidal regions. Its basic outline varies from elongate and narrow, the zygomatic width less than or equal to the mastoid width, to short and comparatively broad with the zygomatic width exceeding the mastoid width of the skull. The braincase is generally elongate and never globose, and in some species is somewhat inflated. Sagittal and lambdoid crests are usually present and in the larger species are often greatly developed. The interorbital region is usually markedly constricted but exceptionally is broader with no sharp constriction between the braincase and the rostrum. The supraorbital ridges in some species are low and poorly defined and in others are well defined and prominent : they may partially enclose a frontal depression, itself sometimes absent. The rostrum, rounded in outline in some species, is in others more markedly pentagonal. It exhibits paired, inflated rostral eminences anterior to the anteorbital region, separated from each other by a shallow groove. The rostrum is expanded laterally to a greater or lesser

degree, and in some species is markedly flattened and more greatly ossified. Considerable variation is displayed in the form of the premaxillae, which basically form a projecting structure with a V-shaped or U-shaped junction with the maxillae. Considered together, they vary from a narrow oblong structure not greatly expanded posteriorly at its junction with the maxillae to a wide structure almost filling the anterior palatal emargination with a wide, sometimes fan-shaped union with the maxillae. Their lateral edges may be deeply notched so that with the maxillae they form the walls of the anterior palatal foramina. In some species, delicate anterior enclosing processes are developed to form the anterior walls of these foramina : these processes in other species completely enclose the foramina which are thus contained within the premaxillae. The anterior palatal foramina in some species are small and rounded and in others are large and oval, elongate or slit-like. The palate is short and broad, the palation usually more or less U-shaped or square, with or without a median emargination or post-palatal spicule. The mesopterygoid fossa is wide and the pterygoids vary considerably in relative length between species. The sphenoidal bridge, flanked by rounded or elongate lateral apertures, usually partially conceals them but in some species is very markedly constricted. A sphenoidal depression is usually present. The cochleae typically are approximately equal in width to their distance apart but exceptionally may be greatly enlarged so that their width is equal to six or eight times this distance. The upper incisors are usually bilobed : the outer lobe, however, is present in varying degrees of obsolescence and in some species is virtually obsolete. The upper canines sometimes have low anterior or posterior cusps. The anterior upper premolar (pm^2) is small or minute, often extruded outwards from the toothrow so that the canine and the second upper premolar (pm^4) are in contact or nearly so : rarely the anterior upper premolar (pm^2) is absent. The posterior cusp of the third upper molar is usually obsolescent or obsolete and its third commissure undeveloped, with the W-pattern of the tooth incomplete : exceptionally the third cusp may be more or less unreduced and the commissure present with the W-pattern of the tooth virtually complete. The crown area of the outer lower incisors in some species is less than or equal to the crown area of the inner teeth : in other species it is greater than the crown area of the inner teeth. The anterior lower premolar (pm_2), sometimes almost equal in size to the second lower premolar (pm_4), is more usually reduced, sometimes to one quarter or one third the size of the second tooth.

Supraspecific groupings within the genus

Tate (1941 : 355) has rightly pointed out that the characters of the numerous species currently included within *Hipposideros* seldom combine to indicate clearly evident evolutionary trends. As this author says, such evidence in this genus is perplexing and often contradictory, and the morphological criteria in *Hipposideros* apparently represent tendencies latent in perhaps all of its species, active in some and quiescent in others. Similarly, such criteria combine but rarely to form an aggregate of features defining natural groups of species within the genus. Despite this, Peters (1871a) was able to discern twelve subgenera in *Hipposideros* (albeit

with fewer species under consideration than are currently included in the genus) and Tate (1941) was able to reduce these only to eleven major species groups, while Aellen (1954) has added a further group to those defined by Tate. A review of the morphological features of these groups indicates that considerable similarity exists between several of them, and that some at least may be separated only with difficulty from each other. It is clearly evident that the great degree of subdivision advocated by Peters is wholly unjustified and that subgeneric division at this level is unwarranted.

It is possible to discern three primary divisions in *Hipposideros*. One, in general a more primitive section, appears to represent the basic group of the genus from which the other, more specialized sections have been derived. It has itself developed a number of specialized forms as well as retaining species exhibiting comparatively simple and unspecialized features. Members of the groups allocated to this section of the genus are generally of small size, with broad, usually rounded ears, often modified by the presence of an internal fold or thickening at the antitragal lobe, while in most the noseleaves are comparatively simple. Lateral supplementary leaflets may be absent: one leaflet may be incipient or present and in some two lateral leaflets are to be found. The skull is more or less elongate and narrow, with an inflated braincase, the zygomatic width less than or not greatly exceeding the mastoid width. The upper incisors are usually weak and lack much of their outer lobe, while the crown dimensions of the outer lower incisors only exceptionally greatly exceed those of the inner lower incisors. The *megalotis*, *bicolor*, *calcaratus* and *galeritus* groups of Tate (1941) and the *curtus* group of Aellen (1954) fall into this division. Of these, the *megalotis* group, containing only the African species *megalotis*, is perhaps the most primitive. Despite the uniquely conjoined ears of *H. megalotis* and its large outer incisors, which in crown area greatly exceed the inner incisors, such characters as its small, simple noseleaf lacking lateral leaflets, and its elongate skull with inflated braincase and weak upper incisors suggest that it is not far removed from the basal stem of *Hipposideros*. The *bicolor* and *calcaratus* groups of Tate (1941) are for the most part little more specialized, their species usually with simple noseleaves which either lack lateral leaflets or have one leaflet only, sometimes in incipency. They have an elongate, narrow skull similar in outline to that of *H. megalotis*. The *galeritus* group of Tate (1941) represents a more specialized derivative of *bicolor*, its species with two lateral leaflets and a more specialized, shorter, wider skull. The *bicolor* and *galeritus* groups as understood by Tate (1941) include a number of isolated species, usually monotypic and in some cases displaying complex developments of the noseleaves. These, although in some instances representing independent but relatively minor lines of modification, in others are highly specialized offshoots of the *bicolor* and *galeritus* types, or of the stem connecting them. In many respects such species connect the two groups, while the *calcaratus* group appears to be a derivative of the *bicolor* type. In the present work, the *bicolor*, *calcaratus* and *galeritus* groups as they are defined by Tate (1941), together with the *curtus* group of Aellen (1954), are united to form a single group, for which the earliest name is *bicolor*.

The second primary division of the genus contains only the highly specialized *cyclops* and *muscinus* groups of Tate (1941), here united to form a group for which *cyclops* is the prior name, restricted to Papua, northern Australia and West Africa. This group exhibits modifications of the noseleaves so peculiar that despite the curious distributional pattern of its members they must be considered to share a common if remote origin. It shares some features with the *bicolor* group, notably the small size of some of its members, but the species allocated to the *cyclops* group have longer, narrower ears, sharply triangular, with little or no antitragal modification. Their noseleaves have two lateral leaflets and are uniquely distinguished in the genus by the second lateral leaflet, which forms an integral part of the posterior leaf and in Australasian species extends anteriorly beneath the anterior leaf, over the upper lip. The noseleaves are further specialized by the development of median tubercles or club-like processes from the intermediate and posterior noseleaves. The skull is less elongate and comparatively wider than in the *megalotis* and *bicolor* groups: the upper incisors are weak and the outer lower incisors are very slightly larger in crown area than the inner lower incisors. The least specialized members of the group share some degree of affinity with the *bicolor* group and it seems likely that the origins of the *cyclops* group lie remotely with the *bicolor* group of species.

A third division of *Hipposideros* is represented by the *pratti*, *armiger*, *speoris*, *diadema* and *commersoni* groups of Tate (1941). Their members are characterized principally by their larger size, their smaller, triangular ears, which usually lack any antitragal modification, by their comparatively simple noseleaves, which have two or more commonly three or four lateral leaflets, and by their comparatively shorter, broader skulls, which have wider, more expanded zygomata. In the species allocated to these groups the upper incisors are stout and retain much of the outer lobe, while the crown area of the outer lower incisors is greater than that of the inner lower incisors, sometimes greatly so. Monotypic species are rare among these groups, and there are no species with the exotic modifications such as are to be found in the first and second divisions. There are, however, some indications of specialization in the presence of greatly developed transverse supplementary lappets behind the posterior leaf in the *pratti* group and in the slightly trilobate posterior leaf of the *armiger* group. The *commersoni* group of Tate (1941) appears to be the African representative of the Austro-Malayan *diadema* group as understood by that author, and in the present work these have been united to form a single group for which the prior name is *diadema*.

The primary divisions of the genus indicate three general but distinct evolutionary trends within *Hipposideros*. One, exemplified by the *megalotis* and *bicolor* groups, is towards small or medium size and development and proliferation of the noseleaves, combined with a corresponding increase in the size of the ears and only exceptionally with extensive cranial modification, the skull generally elongate and not greatly widened. The aberrant *cyclops* group represents a second trend sufficiently differentiated as to justify its separation from that shown by *megalotis* and *bicolor*, with greatly developed noseleaves and much modification of the ears and auditory region of the skull. This group displays a number of unique features, especially in the

combination of small size, large ears and complex noseleaves with a broadened skull in its Australasian species and in the combination of large size, large ears and complex noseleaf with a very wide skull in its West African species. A third trend, exemplified by the *pratti*, *armiger*, *speoris* and *diadema* groups, is towards greater size, without extensive increase in the size and complexity of the ears and noseleaf, but with corresponding broadening of the skull. Each of these divisions include subsidiary lines of development, and while this view is perhaps an over-simplification of major evolutionary trends in *Hipposideros* it is clear that the genus cannot be divided readily into more primitive and more advanced groups of species. It can only be stated in general terms that these divisions represent three more or less parallel lines of development within the genus. However, the *megalotis-bicolor* section includes a number of species which are not greatly specialized, and is therefore to be regarded as the more primitive. It has at the same time developed species which in many of their features are as highly developed as those included in the *cyclops* section or in the section containing the *pratti*, *armiger*, *speoris* and *diadema* groups. The three primary groups express to some extent at least the major lines of development that have occurred within *Hipposideros*: the divisions between them, however, are not clearly defined and there is manifestly no justification for the extreme subdivision of the genus practised by Peters (1871a) in his recognition of twelve subgenera of *Hipposideros*. The genus appears instead to consist of an aggregation of loosely defined groups of species, each exhibiting varying combinations of characters, some highly specialized. Tate (1941) recognized this and divided the genus into eleven species groups but did not study its African species in detail. In the present work these have been related to Asiatic species groups and through the combination of some of the groups of Tate the varying levels of development within *Hipposideros* have been expressed by the division of the genus into seven species groups, one divided into two subgroups. The groups are listed in the following summary, with their included species, excluding *doriae* Peters, probably identical with *sabanus* and which therefore has been excluded from the following discussion.

megalotis group

megalotis Heuglin

bicolor group

bicolor subgroup

bicolor Temminck

ater Templeton

fulvus Gray

cineraceus Blyth

nequam Andersen

calcaratus Dobson

cupidus Andersen

coronatus Peters

ridleyi Robinson & Kloss

jonesi Hayman

dyacorum Thomas

galeritus subgroup

pygmaeus Waterhouse

galeritus Cantor

breviceps Tate

curtus Allen

fuliginosus Temminck

caffer Sundevall

beatus Andersen

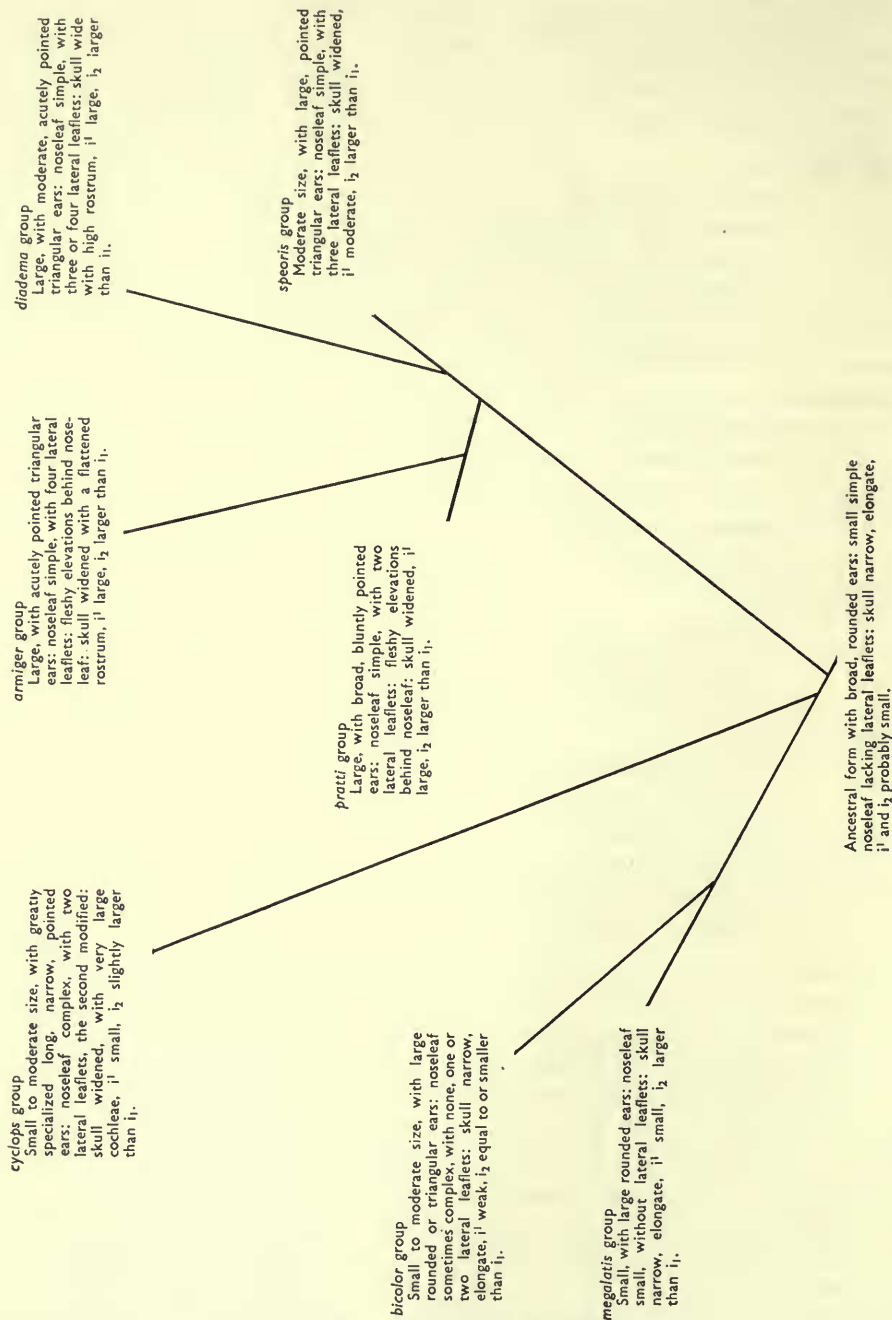
coxi Shelford

papua Thomas & Doria

bicolor group*bicolor* subgroup (*contd.*)*sabanus* Thomas*obscurus* Peters*marisae* Aellen*cyclops* group*cyclops* Temminck*camerunensis* Eisentraut*muscinus* Thomas & Doria*wollastoni* Thomas*semoni* Matschie*stenotis* Thomas*pratti* group*pratti* Thomas*lylei* Thomas*armiger* group*armiger* Hodgson*turpis* Bangs*speoris* group*abae* Allen*larvatus* Horsfield*speoris* Schneider*diadema* group*lankadiva* Kelaart*schistaceus* Andersen*diadema* Geoffroy*dinops* Andersen*inexpectatus* Laurie & Hill*commersoni* Geoffroy

Forty-three species are recognized, of which it has been possible to examine all but *coronatus* and *marisae*. The *bicolor* group as here understood includes the *bicolor*, *galeritus* and *calcaratus* groups of Tate (1941) and is a complex of related species not readily separable into different groups. The *cyclops* group listed by Tate (1941) has been incorporated into the *muscinus* group as recognized by that author to form a *cyclops* group, while the *commersoni* group of Tate (1941) is closely related to the *diadema* group and has been united with it. Relationships between the groups are briefly summarized in the form of a diagram (Fig. 1).

The genus is remarkable for its high content of monotypic species, with no fewer than twenty-seven of its forty-three species not divided into subspecies. Of the remainder, seven are divided into two subspecies and one into three, while only eight species have more than three subspecies. The distribution of subspecies in the species groups of *Hipposideros* is shown in Table 1. The *megalotis*, *bicolor* and *cyclops* groups contain by far the majority of monotypic species and while some of

FIG. 1. Group relationships in *Hipposideros*

these are clearly closely related, others are separated from each other by very distinctive external and cranial features. Rather than representing comparatively recent developments within the genus, from the wide divergence of their isolating characters and their usually restricted distribution, these species appear to be relicts of a rather remote phase of radiation within *Hipposideros*. The three species groups themselves support this contention, their considerable dissimilarities suggesting their separation at an early stage in the evolution of the genus. The *megalotis* group is monotypic and of very restricted distribution, while the *bicolor* group contains a wide diversity of loosely allied species, few of them successful and widespread, and many apparently representing independent lines of development. These groups are widely separated from the *cyclops* group, also of restricted distribution and so distinctively specialized as to demand a long period of modification. The *bicolor* and *cyclops* groups have both Asiatic and African representatives, whose wide separation from each other in a number of basic features indicates that the partition of each parent group into Asiatic and African sections now no longer continuous was evidently a remote event. African representatives of the *bicolor* group are rather less distantly removed from their Asiatic congeners than are the African *cyclops* and *camerunensis* from the Australasian *muscinus* and its allies and the *bicolor* group includes a few species demonstrating to a limited extent the connection between its Asiatic and African species. However, the evidence of this connection is tenuous and the development of the group in the Asiatic and African regions apparently represents two independent, parallel lines of modification from a common but remote origin, often displaying considerable similarity and convergence, and with a number of independent offshoots in each region.

Group	Number of species	Number of monotypic species	Number of species divided into two subspecies	Number of species divided into three subspecies	Number of species divided into more than three subspecies
<i>megalotis</i> group	1	1	—	—	—
<i>bicolor</i> „	23	16	3	—	4
<i>cyclops</i> „	6	6	—	—	—
<i>pratti</i> „	2	2	—	—	—
<i>armiger</i> „	2	—	1	1	—
<i>speoris</i> „	3	1	1	—	1
<i>diadema</i> „	6	1	2	—	3
Totals	43	27	7	1	8

TABLE 1. Distribution of species and subspecies among the species groups of *Hipposideros*.

HIPPOSIDEROS MEGALOTIS group

This group contains only the isolated African species *Hipposideros megalotis* (Heuglin), which may be distinguished at once from all other species of the genus by the low band of integument uniting the ears at their base. Peters (1871a : 329) proposed subgeneric recognition for *megalotis* under the name *Syndesmotis*, largely on account of its conjoined ears, but Dobson (1878 : 151) ignored this separation and concluded from an examination of the type specimen that the species belonged to that section of *Hipposideros* typified by *H. bicolor* and its associated species. Senna (1905 : 275) provided a detailed account of two topotypical specimens of *megalotis* and raised *Syndesmotis* of Peters to generic rank. His diagnosis of *Syndesmotis* was the first comprehensive definition to appear and was based on the conjoined ears, notched, sinuous upper edge of the posterior noseleaf, low cranium, undeveloped sagittal crest, high occipital, elevated frontal, narrow basioccipital and the absence of the anterior upper premolars (pm^{2-2}) in *megalotis*, characters which he considered to render the species generically distinct from *Hipposideros*. However, apart from the first, these features are to be found in one or other of the remaining species groups of *Hipposideros*, and no later author has employed *Syndesmotis* in the subgeneric or generic sense. Tate (1941 : 357) first listed the species as *H. (Syndesmotis) megalotis* and postulated a relationship to the Megadermatidae but later (1941 : 359) listed *megalotis* as the sole species of the *megalotis* group. Hayman (1954 : 285) reviewed earlier accounts of the species, which hitherto had been known only from the type locality, Kérén, in Eritrea, and extended its range to the Kenya highlands. Later (1960 : 61) the same author recorded the species from Ethiopia.

There is little to justify the separation of *megalotis* from *Hipposideros*. Despite its uniquely specialized ears, and its expanded bullae, which are reminiscent of the *cyclops* group, *megalotis* is clearly a primitive species of the genus, allied in many respects to the less specialized species of the *bicolor* group. Such characters as its small, simple noseleaf lacking lateral leaflets, elongate skull with inflated braincase and narrow rostrum and its weak upper incisors display its affinities with *H. bicolor* and its allies. At the same time, an evidently long period of modification has led to the development of a greatly specialized auditory region, and to specialization of the dentition in the loss of the anterior upper premolars (pm^{2-2}) and considerable increase in the dimensions of the outer lower incisors, which greatly exceed the inner lower incisors in crown area. These features, together with its uniquely joined ears, adequately justify the position of *megalotis* as the sole member of an individual group of *Hipposideros*.

Hipposideros megalotis (Heuglin)

Phyllorhina megalotis Heuglin, 1862 : 4, 8, Kérén, Eritrea.

The ears of *Hipposideros megalotis* are large, rounded, their posterior margins without a concavity behind the tip, and have a small internal fold at the antitragal lobe : they are haired for a little less than one half of their length. They are joined

at the base by a low band of integument. The noseleaf is small and simple, and lacks lateral leaflets : the anterior leaf is unemarginated, the intermediate part of the leaf uninflated, with a low median eminence, while the posterior leaf is moderate, supported by three poorly defined ridges and with its upper edge slightly sinuous, more or less semicircular. The skull is small and elongate, with an inflated braincase and narrow rostrum. The sagittal crest is low and there are no supraorbital ridges. The frontal region is slightly elevated and lacks a frontal depression : the rostral eminences are moderately inflated. The zygomata are moderate, with a low jugal projection : the zygomatic width is less than the mastoid width. The anteorbital foramina are large and rounded, closed by a narrow bar of bone. The junction of the premaxillae with the maxillae is U-shaped and the incisive foramina are rounded and not enclosed within the premaxillae, their antero-posterior walls formed by the maxillae. The palation is U-shaped, with a median emargination, and the vomer projects slightly into the mesopterygoid fossa. The sphenoidal bridge is moderate and flanked by large, rounded lateral apertures. There is a shallow sphenoidal depression : the basioccipital is narrow and the cochleae large, their width equal to approximately three times their distance apart. The upper incisors are widely spaced and weakly bilobed, the outer lobe a little smaller than the inner lobe. The upper canines are slender, with a well-developed posterior cusp. The anterior upper premolar (pm^2) is absent and the posterior ridge of the third upper molar obsolescent. The outer lower incisors are much larger in crown area than the inner pair and the anterior lower premolar (pm_2) is one half the height and three quarters or more the length of the second lower premolar (pm_4).

APPROXIMATE DISTRIBUTION : Eritrea ; Ethiopia ; Kenya.

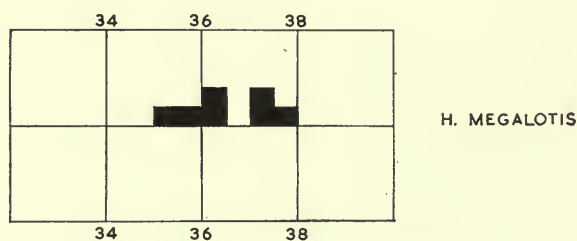


FIG. 2. Length of forearm in *Hipposideros megalotis*

HIPPOSIDEROS BICOLOR group

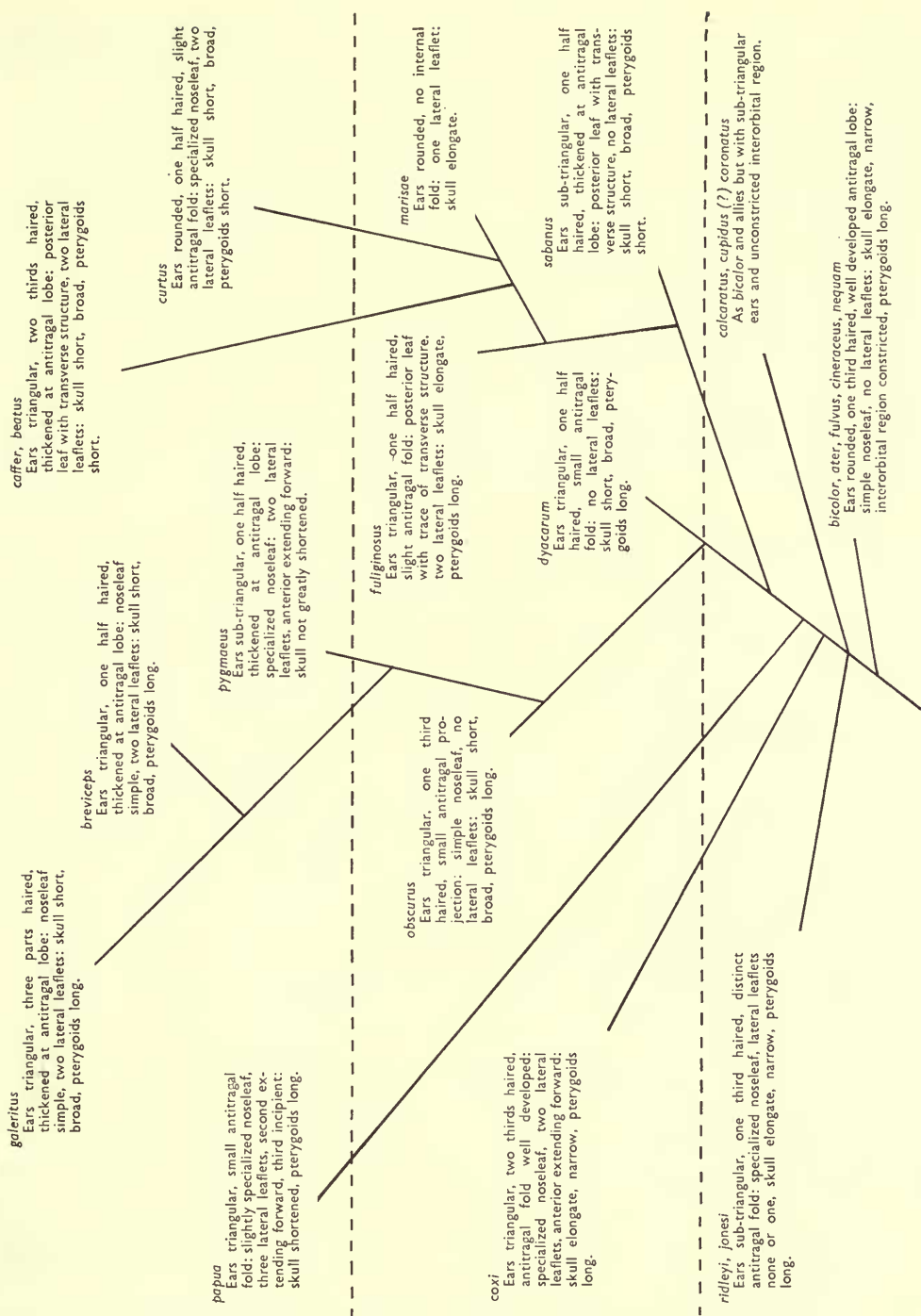
The *bicolor* group as here understood contains the *bicolor*, *calcaratus* and *galeritus* groups of Tate (1941) together with a number of species not studied or allocated to group by that author. The ears of members of the *bicolor* group are large, broad, rounded or more or less triangular in outline, bluntly pointed, with an internal fold or a thickening of the membrane of the ear at the antitragal lobe. Noseleaves within the group vary from the relatively unspecialized and simple structures of *bicolor* and its immediate allies to the complex, greatly developed, sometimes bizarre foliations of such species as *jonesi* or *coxi*. The number of lateral supplementary leaflets varies from none or incipiently one in the more primitive species

of the group to one or more usually two in those more specialized, while *papua*, a somewhat anomalous species allocated to the *bicolor* group, has an incipient, very poorly developed third leaflet. Species allocated to this group have elongate, narrow skulls, with moderately inflated braincases and narrow rostra and an unspecialized auditory region, the cochleae never more than a little wider than their distance apart. Their upper incisors are weak, the outer lobe obsolescent or obsolete, while the crown dimensions of the outer lower incisors are less than or only slightly greater than those of the inner lower incisors. There is no good reason to divide the *bicolor* group into separate species groups: the *bicolor* and *calcaratus* groups of Tate (1941) clearly represent an aggregation of more primitive species while the *galeritus* group and its derivatives as understood by that author consists of more specialized species whose connection with *bicolor* and its immediate allies in some cases can still be traced. The group is of remote origin and is the most wide-ranging of the genus, distributed in one form or another from Africa to the New Hebrides and northern Australia, although it is almost equalled in this respect by the *diadema* group, which has a similar distributional pattern but extends eastward only to the Solomon Islands and does not enter Australia. It is by far the largest group within the genus and while it includes a number of unspecialized species, the group at the same time includes species which have developed this basic pattern into highly specialized elaborations.

The species allocated to the *bicolor* group may be divided into two loosely defined subgroups, corresponding approximately to the *bicolor* and *galeritus* groups of Tate (1941). The *bicolor* subgroup includes the *calcaratus* group of Tate (1941), which has few characters to distinguish it from *bicolor* and its allies, and is predominantly Indo-Australian in distribution, with two species extending its distribution to Africa. Its members are in general less specialized than those of the *galeritus* subgroup and usually have broader, more rounded ears, which in most cases have an internal fold at the antitragal lobe and are haired for one half or less of their length. Lateral supplementary leaflets as a rule are absent or are exceptionally represented by a single small leaflet. The skull is elongate and narrow, with an inflated braincase, the zygomatic width rarely exceeding the mastoid width. Although the subgroup includes some of the least specialized species of the genus, it contains also such more advanced derivatives as *dyacorum*, *sabanus* and *jonesi* exhibiting a considerable degree of specialization. The *galeritus* subgroup is represented in the Asiatic and Australasian regions by *galeritus* and its associated species and in the Ethiopian region by *caffer* and its allies. Its members are characterized by their usually more or less triangular ears, which often display a concavity in their posterior margins just behind the tip of the ear. The antitragal fold is less prominent and the ears are usually haired for about two thirds of their length. The noseleaves are in general more specialized and have two or exceptionally three lateral supplementary leaflets. Members of this subgroup have shorter, broader skulls than the members of the *bicolor* subgroup, with the zygomatic width exceeding the mastoid width. As in the *bicolor* subgroup, some species of the *galeritus* subgroup exhibit great elaboration of its basic pattern.

No definitive line of separation can be found between the subgroups, and they are linked by species exhibiting their respective characteristics in differing combinations. *Hipposideros sabanus* and *H. dyacorum* both lack lateral leaflets and have the comparatively simple noseleaf of the *bicolor* subgroup yet have the shortened, rather broadened skull characteristic of the *galeritus* subgroup. *Hipposideros obscurus* has likewise no lateral leaflets but has somewhat triangular ears and a short, broad skull. *Hipposideros marisae* has ears and noseleaf similar to those characteristic of the *galeritus* subgroup, but has one lateral supplementary leaflet and a somewhat elongate skull. *Hipposideros curtus* has two lateral leaflets and cranially resembles the *galeritus* type, but has the ears haired for only one half of their length. *Hipposideros fuliginosus* and *H. pygmaeus* have two lateral leaflets but have the sparsely haired ears and elongate skulls of the *bicolor* type, while *H. coxi* has two lateral leaflets and ears haired for two thirds of their length yet has an elongate, unbroadened skull. Such species serve to demonstrate the close affinity of the members of the *bicolor* group and its essential unity. This treatment of the group greatly extends the views of Tate (1941 : 358, 366) who recognized that the African *caffer* and its allies should be associated with his Asiatic *galeritus* group, but did not relate these species and their associates to those he included in the *bicolor* group as he defined it. The allocation of the African species of the *bicolor* group as here understood contrasts sharply with the views of Aellen (1952 : 62), who divided them widely by the recognition of a *caffer* group for *caffer* and its associated species *curtus*, *fuliginosus* and *beatus*, and later (1954 : 479, 480) recognized additionally a *jonesi* group for the sole species *jonesi* and a *curtus* group for the species *curtus* and *marisae*. *Hipposideros caffer* and its allies, together with *curtus*, are closely related to *galeritus*, and in the present work are referred to the *galeritus* subgroup, while *jonesi* and *marisae* have affinities with the *bicolor* subgroup, to which they are referred.

Possible relationships within the group are summarized in the form of a diagram (Fig. 3). Morphological characters in the group rarely combine to indicate definite trends, and the relationships of the numerous species comprising the *bicolor* group are not easily discerned and are difficult of definition. The considerable degree of elaboration of the noseleaves displayed by some species tends further to obscure their basic pattern. General tendencies discernible within the group are for the ears to become less rounded and more triangular, and for their posterior edges to develop a concavity just behind the tip. At the same time, an increase in the area of body fur extending over the outer surface of the ears can be seen, and the internal fold tends to become less prominent. Lateral supplementary leaflets are absent in the more primitive species of the group, more advanced species having one or more frequently two leaflets, while one species, *papua*, possesses a third leaflet, incipient and poorly developed. Cranially, the elongate, rather narrow outline of the skull in the primitive members of the group tends to become shorter and broader in those more advanced. These general trends, however, are obscured to a large extent by considerable overlap between a number of species, indicated in fig. 3 by enclosure between two parallel dotted lines. Such species exhibit varying combina-

FIG. 3. Possible relationships in the *Hipposideros bicolor* group

tions of primitive and advanced morphological characters and must be regarded as transitional between the simplest members of the group and those most specialized, although some such as *coxi* display a high degree of individual specialization. A number of less general trends exist within the group and are confined in some cases to one or two species. Such a trend is found in *ridleyi* and *jonesi*, large species of the *bicolor* subgroup which have however developed the internarial septum to form a concave circular disc between and partially covering the nostrils: *jonesi* is more developed in this respect and additionally has a deeply pocketed posterior leaf reminiscent of that of *coxi*. Similarly, *calcaratus* and *cupidus* have developed a broad interorbital region and their zygomata are widened to an extent considerably exceeding the mastoid width, although in other respects both are very simple species with broad ears which possess an antitragal fold and with a simple noseleaf, lacking lateral leaflets. *Hipposideros coxi* has a highly complex noseleaf with two lateral leaflets, the anterior leaflet extending forwards beneath the anterior leaf to the median line and with the posterior leaf elaborated into a complex, deeply pocketed structure. Its skull, however, is comparatively elongate and narrow and basically is of the *bicolor* type. A trend towards *galeritus* is characterized by the retention of a skull architecturally rather like that of the *bicolor* type, although broadened, with long pterygoids and a short sphenoidal bridge. It can be traced through *dyacorum*, a simple species lacking lateral leaflets and with a comparatively elongate skull, *obscurus*, a species with a specialized noseleaf, no lateral leaflets and shortened skull and *pygmaeus*, similar to *obscurus*, but with a more specialized noseleaf and two lateral leaflets. The trend towards *caffer* is characterized by a shortening of the pterygoids and consequent extension of the sphenoidal bridge, and in some species by the development of a transverse, serrated structure from the rear face of the posterior leaf. It includes *sabanus*, a simple species lacking lateral leaflets but with a transverse supplementary structure behind the rear leaf and a short, broad skull with short pterygoids and *fuliginosus*, with two lateral leaflets, a trace of a supplementary structure behind the posterior leaf yet with an elongate skull with long pterygoids. This trend must include also *marisae*, with broad ears, one small leaflet and elongate skull, and *curtus*, with similar ears, two lateral leaflets and shorter, broadened skull with short pterygoids, two species further specialized by the considerable inflation of the internarial septum. *Hipposideros papua*, apparently derived from the stem leading to *galeritus* and *caffer*, is a highly specialized species unique in the *bicolor* group by the possession of three lateral supplementary leaflets, the third small and undeveloped. The anterior leaflet extends upwards towards the base of the posterior leaf: the second or central leaflet extends anteriorly beneath the anterior leaf but does not reach the median line. The ears are acutely pointed but lack a concavity in their posterior margins. The skull is short and broad, with a very wide rostrum and long pterygoids.

The *bicolor* group contains a high proportion of monotypic species, with only *ater*, *bicolor*, *galeritus* and *caffer* of widespread distribution and divisible into a number of clearly defined subspecies while *fulvus* and *cineraceus* are each divisible into two subspecies but are much less widely distributed. The remaining species are

monotypic and while this may in part be due to the inadequacy of collections, there seems little doubt that this feature, with their sharply distinct morphological separation from each other in many cases and their restricted distribution, is an indication that some at least are relict forms that have survived the competition of the more successful species either by considerable specialization or in restricted habitats. Predominantly Indo-Australian in distribution, in Africa the group has rarely given rise to such highly specialized forms as *pygmaeus*, *coxi* and *papua*, and apart from *jonesi* forms a more closely related aggregation of species than those of the Indo-Australian region. However, the African representatives of the group have been isolated for a considerable period as is demonstrated by the great development of the noseleaf of *jonesi* when compared with that of *ridleyi* and by the structural differences in the posterior noseleaf and skull of *caffer* and its allies with those of *galeritus* and its associated species. Lack of diversity might be expected on a large land mass such as Africa : the island habitats of Indo-Australia have evidently encouraged diversification and have enabled species such as *dyacorum*, *sabanus*, *obscurus*, *pygmaeus*, *coxi* and *papua* to survive.

Hipposideros bicolor (Temminck), 1834, appears to be the first identifiable name in the group and is therefore adopted as the group name. Lesueur & Petit, in Péron, Voyage de Découvertes aux Terres Australes, Atlas, 1807, pl. 35 (volume not dated, date taken from Sherborn (1925 : 1661) : discussed by Oey & Feen (1958 : 230)) figured three bats from Timor under the name *Rhinolophe Crumenifère* (*Rhinolophus crumeniferus* N.). The status of this name has been discussed by Tate (1941 : 367 (footnote), 382), Laurie & Hill (1954 : 56) and Oey & Feen (loc. cit.). It is usually ascribed to Péron, the author of the text of the Voyage de Découvertes aux Terres Australes : however *Rhinolophus crumeniferus* is based solely on plate 35 of the Atlas, the title page of which clearly attributes this part of the work to Lesueur & Petit. Tate (1941 : 382) considered the plate to depict bats of the genus *Hipposideros* "probably related to *galeritus* and *cervinus*" while Laurie & Hill (loc. cit.) concluded that the bats represented were most nearly allied to *cervinus* (here considered to be a race of *H. galeritus*), an opinion supported by Oey & Feen (loc. cit.). The plate by Lesueur & Petit portrays bats with broad, triangular ears, which have a concavity in their posterior margins and with two lateral supplementary leaflets, thus referable to the *bicolor* group. The ears, however, are not noticeably covered with body fur. The anterior noseleaf is simple and the internarial septum is not inflated while the posterior leaf is high, supported by three well-defined septa not quite reaching the upper edge of the leaf, which is semicircular in outline. The leaf is largely unpigmented and there is a large frontal sac. It seems likely, therefore, that the three bats depicted by Lesueur & Petit represent *H. galeritus cervinus* or a closely related form. Tate (1941 : 387) postulates affinity with *H. papua* but the second leaflet shown in the plate by Lesueur & Petit does not extend forward beneath the anterior part of the horseshoe and these authors portray no incipient third leaflet. Pending discovery of the type or the collection of topotypes, the name must remain *incertae sedis*.

The species here allocated to the *bicolor* group (with the exception of *coronatus*, which from its description is evidently near to *calcaratus*, and *doriae*, probably synonymous with *sabanus*) may be keyed :

- 1 Lateral supplementary leaflets none or one 2
Lateral supplementary leaflets two or three 14
- 2 Anterior upper premolar (pm^2) obsolescent or obsolete, if present minute, extruded from toothrow, with second upper premolar (pm^4) and canine in contact, anterior lower premolar (pm_2) one quarter the length and one third or less the height of the second lower premolar (pm_4) 3
Anterior upper premolar (pm^2) present, never minute, anterior lower premolar (pm_2) one third or more the length and height of second lower premolar (pm_4) 4
- 3 Anterior leaf without a median emargination : posterior leaf supported by a well-defined median septum and weaker lateral septa : pterygoids long, sphenoidal bridge wide *dyacorum* (p. 43)
Anterior leaf with well-defined median emargination : posterior leaf lacking supporting septa : pterygoids short, sphenoidal bridge narrow *sabanus* (p. 44)
- 4 Internarial septum expanded to form a more or less disc-like structure between the nostrils : one lateral supplementary leaflet, sometimes rudimentary 5
Internarial septum not greatly expanded or modified, more or less parallel sided : no lateral supplementary leaflets 7
- 5 Internarial septum expanded to form a concave sub-circular disc 6
Internarial septum expanded to form an ellipsoidal structure *marisae* (p. 48)
- 6 Posterior leaf low, rounded above : lateral supplementary leaflet incipient, barely visible : palation U-shaped, without a post-palatal spicule *ridleyi* (p. 39)
Posterior leaf high, sub-triangular above : lateral supplementary leaflet well developed, extending anteriorly beneath anterior leaf to median line : palation square, with a small post-palatal spicule *jonesi* (p. 40)
- 7 Interorbital region wide, not sharply constricted, its width nearly equal to that of the rostrum 8
Interorbital region decidedly constricted, its width considerably less than that of the rostrum 9
- 8 Sphenoidal bridge well developed, broad, partially concealing small, elongate lateral apertures : well developed sphenoidal depression *calcaratus* (p. 37)
Sphenoidal bridge narrow, not concealing large, rounded lateral apertures : poorly developed sphenoidal depression *cupidus* (p. 38)
- 9 Anterior leaf without a median emargination : posterior leaf with three supporting septa : no glandular ridge on muzzle beneath margin of anterior leaf 10
Anterior leaf with small median emargination : posterior leaf without supporting septa : a low glandular ridge on muzzle beneath margin of anterior leaf *obscurus* (p. 47)
- 10 Internarial septum thickened and bulbous : anterior half of zygomata slender 11
Internarial septum uninflated : anterior half of zygomata massive 12
- 11 Superior projection of zygomata lacking or poorly developed : anterior upper premolar (pm^2) not extruded from toothrow *cineraceus* (p. 35)
A low superior zygomatic projection : anterior upper premolar (pm^2) extruded or partially extruded from toothrow *ater* (p. 30)
- 12 Posterior projecting portion of vomer blade-like 13
Posterior projecting portion of vomer thickened *bicolor* (p. 25)
- 13 Anterior lower premolar (pm_2) much reduced, one third the length of second lower premolar (pm_4) *fulvus* (p. 33)
Anterior lower premolar (pm_2) less reduced, one half the length of second lower premolar (pm_4) *nequam* (p. 36)

- 14 Anterior lateral supplementary leaflet extending anteriorly beneath anterior leaf to the median line 15
 Anterior lateral supplementary leaflet not extending anteriorly beneath anterior leaf to the median line 16
- 15 Noseleaf not excessively specialized : intermediate leaf without a median eminence : posterior leaf supported by three septa of equal width, not deeply pocketed *pygmaeus* (p. 49)
 Noseleaf greatly specialized : intermediate leaf with prominent median eminence : posterior leaf supported by narrow median septum and two broad lateral septa, deeply pocketed *coxi* (p. 68)
- 16 Second lateral supplementary leaflet not extending anteriorly beneath the anterior leaf : no trace of a third leaflet 17
 Second lateral supplementary leaflet extending anteriorly beneath the anterior leaf : an incipient third leaflet *papua* (p. 70)
- 17 Posterior leaf having a transverse supplementary structure with a serrated upper edge developed from its posterior face 18
 Posterior leaf without a transverse supplementary structure developed from its posterior face or with such a structure low, undeveloped and lacking a serrated upper edge 19
- 18 Anterior upper premolar (pm²) small, slightly extruded from toothrow, or compressed between canine and second upper premolar (pm⁴) *caffer* (p. 62)
 Anterior upper premolar (pm²) minute, extruded from toothrow, canine and second upper premolar (pm⁴) in contact or nearly so *beatus* (p. 66)
- 19 Posterior leaf supported by three septa 20
 Posterior leaf without supporting septa, paired low lateral ridges sometimes present *fuliginosus* (p. 61)
- 20 Internarial septum not expanded : pterygoids long, sphenoidal bridge wide, partially concealing lateral apertures 21
 Internarial septum expanded to form a slightly disc-like structure : pterygoids short, sphenoidal bridge narrow, not concealing lateral apertures *curtus* (p. 60)
- 21 Ears haired for one half of their length : tips of upper incisors strongly convergent *breviceps* (p. 58)
 Ears haired for two thirds of their length : tips of upper incisors not strongly convergent *galeritus* (p. 52)

Hipposideros bicolor

The ears are large and rounded, their anterior margins strongly convex and their posterior margins lacking any concavity just behind the tip. There is a distinct antitragal fold. The noseleaf is simple, of moderate size, and lacks lateral supplementary leaflets. The internarial septum is more or less triangular, broad at the base, narrowed between the nostrils, very slightly inflated and separated from the lateral parts of the anterior leaf by deep grooves. The lateral parts of the anterior leaf adjacent to the nostrils are not expanded and do not partially conceal the narial openings. The intermediate part of the leaf is unspecialized and the posterior leaf is supported by three septa. The skull is elongate and slender, with a comparatively broad braincase, narrowed interorbital region and slightly inflated rostral eminences. There is a low sagittal crest. The zygomata are massive, with or without a low superior jugal projection, and the anteorbital foramina are rather elongate, closed by a narrow bar of bone. The premaxillae are narrow and taken

together make a wedge-shaped junction with the maxillae. Their anterior enclosing processes are delicate and do not enclose the rounded anterior palatal foramina. The palation is shallowly V-shaped and the mesopterygoid fossa is wide, with a projecting, thickened vomer. The pterygoids are long and the sphenoidal bridge wide, partially concealing large, elongate lateral apertures. There is a shallow oval sphenoidal depression and the cochleae are of moderate size, their width a little greater than their distance apart. The anterior upper premolar (pm^2) is very small and is extruded from the toothrow, while the posterior ridge of the third upper molar is reduced to approximately one half of the length of the anterior ridge. The crown area of the outer lower incisors is equal to that of the inner lower incisors or is very slightly greater, while the anterior lower premolar (pm_2) is one half or more the length of the second lower premolar (pm_4) and two thirds to three quarters its height.

Andersen (1918 : 379) provided the first study of the group of species allied to *Hipposideros bicolor*, recognizing among others a small species, *H. cineraceus*, a species of medium size, which he called *H. bicolor* and two larger species, *H. pomona* and *H. gentilis* (here considered to be conspecific) in southeastern Asia. Tate (1941 : 360), however, in the course of revisionary work on the genus, has designated a lectotype for *Rhinolophus bicolor* Temminck, 1834, and has left its exact application in some doubt. The original description by Temminck, 1834, Tijdschr. Natuur. Gesch. 1 (1) : 19, pl. 1, fig. 3 listed no specimens, but Temminck stated that the species was to be found in Java, Amboina and Timor and said that it had been received in considerable numbers at the Netherlands Museum. Later, Temminck, 1835, Monogr. Mamm. 2 : 18 (which Tate apparently thought to be the original description) provided a further, more detailed description, basing it on the examination of ten females and four males, and giving as the provenance of the species the islands of Java, Amboina and Timor. His series is clearly composite, the specimens from Amboina, which Temminck said to be smaller than those from Java being referable to the form subsequently described by Peters (1871a : 323) as *Phyllorhina amboinensis*. Temminck gives measurements of an adult from Java with forearm " 1 pouce 8 lignes " (approximately 43 mm.), perhaps a representative of *H. bicolor* in the sense of Andersen (1918 : 380), a species of medium size widely distributed in the Indo-Australian region.

Jentink (1887 : 272, 1888 : 168) has listed among other specimens in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden, a large part of the series probably forming the basis of the description of *Rhinolophus bicolor* by Temminck. Tate (1941 : 361) has examined these specimens and has designated as lectotype specimen " d " of Jentink (1888 : 168), collected by Van Hasselt (from the collections of Kuhl and Van Hasselt according to Jentink) on the Côte d'Anjer, in the extreme northwest of Java, whence Tate restricts the type locality. This selection introduces a change of name into the group as originally defined by Andersen (1918 : 379) since from the detailed notes on the lectotype provided by Tate, it is evidently a member of the species called *Hipposideros gentilis* by Andersen (1918 : 380), considered by Ellerman & Morrison-Scott (1951 : 127) and in the present study to be conspecific

with *H. pomona*, also proposed by Andersen in this work. *Rhinolophus bicolor* Temminck is by far the earliest name in this section of the genus and as a result must replace *H. pomona* as used by Andersen (1918 : 380) and some subsequent authors. The earliest name identifiable with certainty for the species of medium size called *H. bicolor* by Andersen (1918 : 380) appears to be *Hipposideros ater* Templeton, 1848.

APPROXIMATE DISTRIBUTION : India east to Hainan and the Philippine Islands ; Malay Peninsula, Sumatra, Java and adjacent islands.

Hipposideros bicolor bicolor (Temminck)

Rhinolophus bicolor Temminck, 1834 : 19, pl. 1, fig. 3 ; 1835 : 18 (further description).

Lectotype designated and type locality restricted to Anjer coast, northwestern Java by Tate (1941 : 361).

Hipposideros javanicus Sody, 1937 : 215. Babakan, Kroja, Tjilatjap, central Java.

No Javan specimens are available for study : from Tate (1941 : 361) the lectotype has an elongate skull with slight nasal eminences and a rather pronounced posterior interparietal swelling. The anterior upper premolar (pm^2) is slightly extruded from the toothrow, while the anterior lower premolar (pm_2) is three quarters the height of the second lower premolar (pm_4). Tate suggested that *Hipposideros javanicus* Sody, 1937 might be synonymous with *H. b. bicolor* as represented by the lectotype in Leiden. The measurements of the type specimen of *H. javanicus* as quoted by Sody agree closely with those of the lectotype of *H. b. bicolor* as recorded by Tate.

DISTRIBUTION : Java ; Banka Island.

Hipposideros bicolor pomona Andersen

Hipposideros pomona Andersen, 1918 : 380. Haleri, north Coorg, India.

The zygomata have a low jugal projection and the anterior upper premolar (pm^2) is very small while the anterior lower premolar (pm_2) is one half the length and two thirds the height of the second lower premolar (pm_4).

DISTRIBUTION : Southern India.

Hipposideros bicolor gentilis Andersen

Hipposideros gentilis Andersen, 1918 : 380. Thayetmyo, Burma.

Cranially similar to *H. b. pomona* but the zygomata lack a definite jugal projection. The anterior lower premolar (pm_2) is slightly more than one half the length and two thirds the height of the second lower premolar (pm_4).

DISTRIBUTION : Northern India ; Assam ; Sikkim ; Burma.

***Hipposideros bicolor sinensis* Andersen**

Hipposideros gentilis sinensis Andersen, 1918 : 380. Foochow, Fukien, China.

The anterior lower premolar (pm_2) is three quarters or more the length of the second lower premolar (pm_4), sometimes almost equal to it in length, and is two thirds its height. Cranially, the subspecies otherwise resembles *H. b. gentilis*. Osgood (1932 : 221) suggested that *H. b. sinensis* may be a synonym of *H. b. gentilis*, while Bourret (1942b : 11) considered that *H. b. sinensis* was not a valid subspecies.

DISTRIBUTION : Southern China ; Hainan ; recorded from Hong Kong by Romer (1960 : 2) ; Siam (part) ; Indochina (recorded as *H. gentilis* by Osgood (1932 : 220) and Bourret (1942b : 11 ; 1944 : 6)).

***Hipposideros bicolor atrox* Andersen**

Hipposideros gentilis atrox Andersen, 1918 : 380. Semangko Gap, Selangor, Federation of Malaya, 2,800 feet.

There is a low jugal projection on the zygomata and the sphenoidal pits are very slightly wider than in the foregoing subspecies. The anterior lower premolar (pm_2) is one half or less the length and one half the height of the second lower premolar (pm_4). Davis (1961 : 90) gives a description, with measurements, of a series of *H. b. atrox* from the Federation of Malaya.

DISTRIBUTION : Malay Peninsula ; Terutau Island ; Tioman Island ; Sumatra.

***Hipposideros bicolor major* Andersen**

Hipposideros gentilis major Andersen, 1918 : 380. Bua-Bua, Engano Island, off west coast of Sumatra.

Cranially exactly like *H. b. atrox* with the anterior lower premolar (pm_2) one half the length and height of the second lower premolar (pm_4). Although Andersen in the original description stated that *H. b. major* was larger than *H. b. atrox*, the two subspecies seem likely to prove synonymous.

***Hipposideros bicolor erigens* Lawrence**

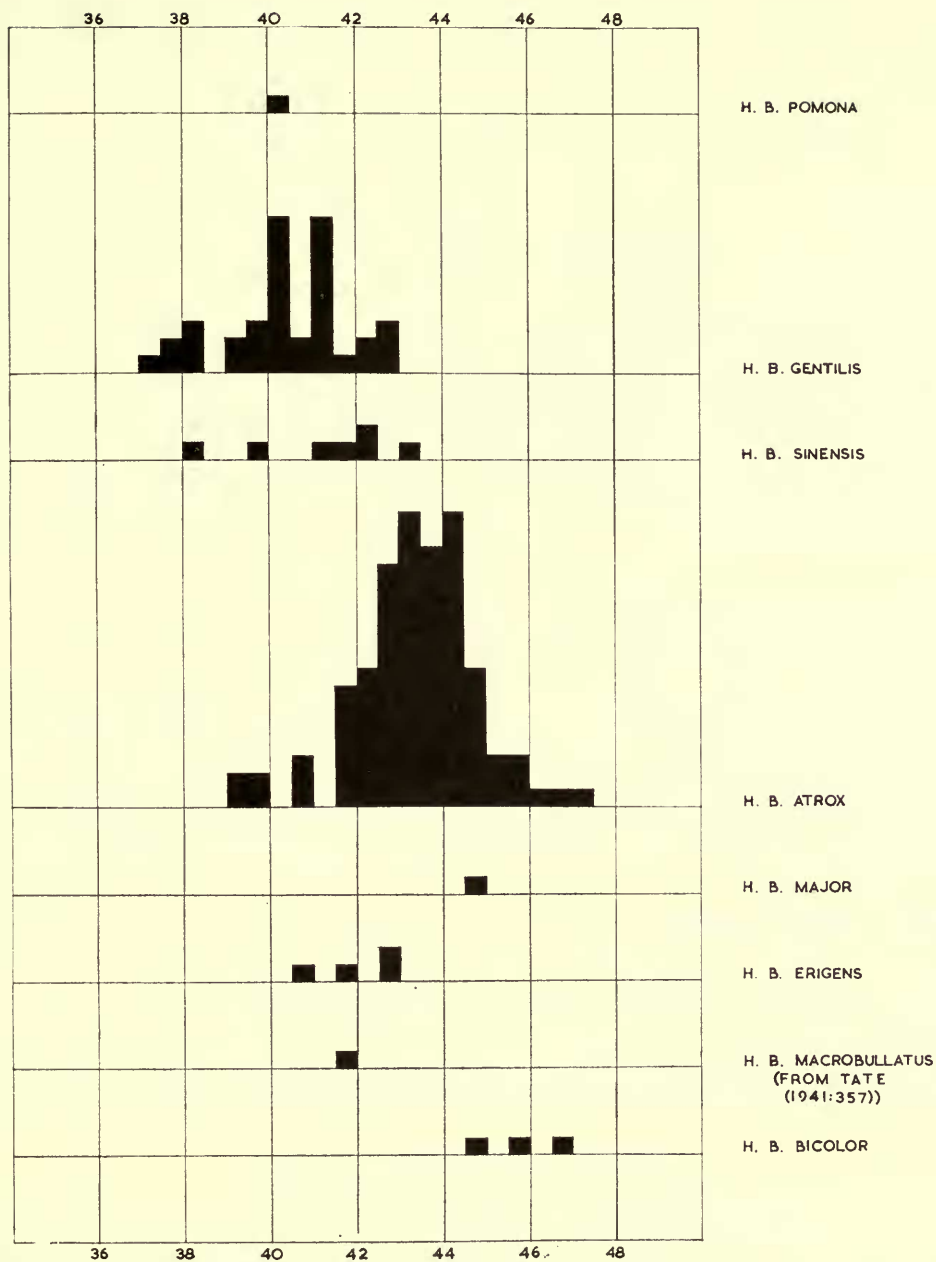
Hipposideros erigens Lawrence, 1939 : 56. Lower slopes of Mount Halcon, northern side, near Calapan, Mindoro, Philippine Islands.

There are no specimens of this form in the collections of the British Museum (Natural History). Its large size, large ears, noseleaf, bullae and teeth suggest alliance with *H. bicolor*.

***Hipposideros bicolor macrobullatus* Tate**

Hipposideros bicolor macrobullatus Tate, 1941 : 357. Talassa, near Maros, south Celebes, 300 metres.

There are no specimens of this form in the collections of the British Museum (Natural History). Its measurements and characters as given by Tate agree closely with those of *H. bicolor*.

FIG. 4. Length of forearm in *Hipposideros bicolor*

Hipposideros ater

The ears and noseleaf are very much like those of *H. bicolor* but the internarial septum is swollen and inflated, slightly bulbous, narrow at its upper end and separated from the lateral parts of the anterior leaf by deep grooves. The narial margins of the anterior part of the leaf are expanded and partially conceal the nostrils. Cranially, there is considerable similarity to *H. bicolor* but the zygomata are slender anteriorly and the vomer projects slightly into the mesopterygoid fossa and is slightly thickened. The anterior upper premolar (pm_2) is usually extruded from the toothrow and the posterior ridge of the third upper molar is one half or less the length of the anterior ridge. The outer lower incisors are very slightly larger in crown area than the inner lower incisors. The anterior lower premolar (pm_2) varies in length from one half or less of the length of the second lower premolar (pm_4) in western subspecies to a length almost equal to that of the second lower premolar in eastern subspecies, while its height is one half to two thirds that of the second lower premolar. Formerly known as *H. bicolor*, this species must now be called *H. ater* since the designation of a lectotype for *Rhinolophus bicolor* Temminck by Tate (1941 : 361) transfers that name to the species formerly called *H. pomona* or *H. gentilis*.

DISTRIBUTION : India to the Philippine Islands, Papua and northern Australia.

***Hipposideros ater ater* Templeton**

Hipposideros ater Templeton, 1848 : 252. Colombo, Ceylon.

Hipposideros atratus Kelaart, 1850a : 208. Substitute for *ater*.

The zygomata have a well developed jugal projection and the posterior ridge of the third upper molar is greatly reduced and obsolescent. The anterior lower premolar (pm_2) is less than one half the length of the second lower premolar (pm_4) and its height is one half or less than that of the second lower premolar. There appears to be no difference between specimens from Peninsular India (called *Hipposideros* (?) *bicolor fulvus* by Ellerman & Morrison-Scott (1951 : 127)) and those from Ceylon.

DISTRIBUTION : Ceylon ; India.

***Hipposideros ater nicobarulae* Miller**

Hipposideros nicobarulae Miller, 1902 : 781. Little Nicobar Island, Bay of Bengal.

Similar to *H. a. ater* but slightly larger, with the anterior lower premolar (pm_2) one half the length of the second lower premolar (pm_4) and one half or less its height.

***Hipposideros ater saevus* Andersen**

Hipposideros albanensis saevus Andersen, 1918 : 380. Kei Islands.

Hipposideros gentilis toala Shamel, 1940 : 352. Toeare, Celebes.

Very similar to *H. a. ater* but a little larger, with the jugal projection of the zygomata very low or lacking. The anterior lower premolar (pm_2) varies from slightly more than one half the length to three quarters the length of the second lower premolar (pm_4), and is one half or slightly more its height.

Andersen (1918 : 380) employed *Rhinolophus bicolor* Temminck, 1834, for a medium sized (forearm 37–42 mm.) species of bat of his *bicolor* group, giving as its provenance Sumatra and Java. In this he was followed by a number of subsequent authors including Chasen (1940 : 44), Ellerman & Morrison-Scott (1951 : 126) and Laurie & Hill (1954 : 54). However, Tate (1941 : 361) has designated as lectotype of *Rhinolophus bicolor* Temminck a specimen from that part of the original series still extant in the Rijksmuseum van Natuurlijke Historie, Leiden. It is obvious from the notes and measurements of the lectotype as quoted by Tate that this specimen is not representative of the species of *Hipposideros* hitherto called *bicolor*. It is a large bat in comparison with the species formerly called *bicolor*, with a forearm of 47 mm., zygomatic width 9.1 mm., greatest mastoid width 9.4 mm., least inter-orbital width 3.0 mm. and c-m³ 6.5 mm. Tate also points out that *Hipposideros javanicus* Sody, 1937, from Java, is very probably synonymous with the species represented by this lectotype. These factors taken in conjunction indicate that the lectotype designated by Tate belongs to the species called *gentilis* by Andersen (1918 : 380) and subsequent authors, and *Rhinolophus bicolor* Temminck, 1834, must therefore be transferred to this species. This leaves the bats from Java and its environs, hitherto called *H. bicolor bicolor*, without a name, and in the ordinary course of events a new subspecific term would be required. However, there seems little to distinguish these bats from *H. ater saevus* : specimens from Java, Sumatra and the Malay Peninsula average very slightly smaller than those from more easterly localities and are a little paler while the anterior lower premolar (pm₂) is slightly more reduced, but these points scarcely seem to warrant subspecific recognition.

Shamel (1940 : 352) described *Hipposideros gentilis toala*, a Celebesian bat which he considered related to the mainland species *gentilis* (= *bicolor* in the present sense). However, Tate (1941 : 361, 390) thought *toala* a probable synonym of *H. a. saevus* : there seems in fact to be little size difference between *toala* and *saevus* (measurements of the type specimen of *toala* as quoted by Tate (1941 : 361) conflict with those given by Shamel in the original description) and in the present study they are considered to be synonymous.

DISTRIBUTION : Mergui Archipelago ; Tenasserim ; Peninsular Siam ; Condor Island ; Federation of Malaya ; Teratau Island ; Tioman Island ; Sumatra ; Java ; Bali ; Celebes ; Peleng Island ; Kei Island ; Buru ; Ceram ; possibly also Sanghir and Talaud Islands. Tate (1941 : 362) states that a specimen in the American Museum of Natural History from Halmahera is identical with one from Java in the Museum of Comparative Zoology, which from the measurements quoted by Tate is apparently an example of *H. ater*.

Hipposideros ater antricola (Peters)

Phyllorhina antricola Peters, 1861 : 709. Paracali, Luzon, Philippine Islands.

Hipposideros wrighti Taylor, 1934 : 237. Baguio, Benguet (near Headwaters gold mine), Luzon, Philippine Islands.

A specimen from Balabac Island (B.M. 94.7.2.51) is referred to this subspecies. It has the anterior lower premolar (pm₂) considerably reduced, one half the length

and height of the second lower premolar (pm_4). Lawrence (1939 : 55) summarizes the taxonomic history of *Hipposideros wrighti* Taylor and concludes that it may be in fact a re-description of *H. a. antricola*.

DISTRIBUTION : Philippine Islands : Luzon ; Marinduque ; Mindoro ; Mindanao (Sanborn (1952 : 104)) ; Palawan (Sanborn (1952 : 104)) ; Balabac.

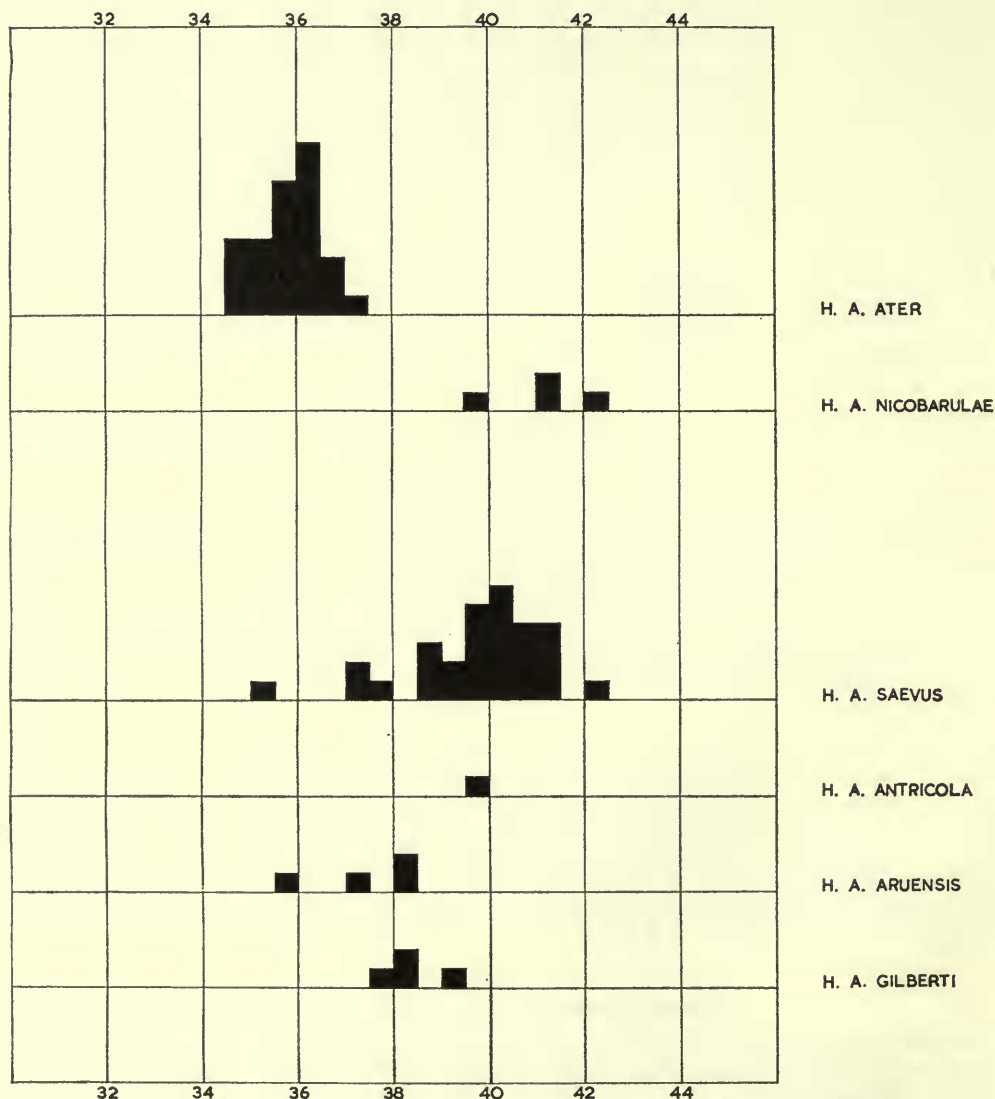


FIG. 5. Length of forearm in *Hipposideros ater*

***Hipposideros ater aruensis* Gray**

Hipposideros aruensis Gray, 1858 : 107. Aru Islands.

Hipposideros albanensis Gray, 1866b : 220. Port Albany, northwest Queensland.

The zygomata bear a small jugal projection while the anterior lower premolar (pm_2) is rather larger than in *H. a. saevus* and is equal or almost equal in length to the second lower premolar (pm_4) and is two thirds its height. The type specimen is the only available example of *Hipposideros albanensis* Gray. Its skull is fragmentary and only the left-hand maxillary toothrow and the mandible remain. The dentition is identical with that of *H. a. aruensis*.

DISTRIBUTION : Aru Islands ; southern and northwestern New Guinea ; northern Queensland.

***Hipposideros ater amboinensis* (Peters)**

Phyllorhina amboinensis Peters, 1871a : 323. Amboina.

There is no example of this subspecies in the collections of the British Museum (Natural History). It is very probably synonymous with *H. a. aruensis* (see Tate (1941 : 380)).

***Hipposideros ater gilberti* Johnson**

Hipposideros bicolor gilberti Johnson, 1959 : 183. Oenpelli, East Alligator River, Northern Territory, Australia (12° 21' S., 133° 04' E.).

The collections of the British Museum (Natural History) contain four topotypes (B.M. 23.5.14.9-12) of this subspecies. They agree closely with the description and measurements given by Johnson : there seems little to distinguish them from *H. a. aruensis* except their slightly paler colour.

Hipposideros fulvus

The ears are very large and rounded, longer than the head, the upper third of their posterior margins very slightly flattened. The noseleaf closely resembles that of *H. bicolor* and has the internarial septum narrow, uninflated, broadened at its base and narrowed between the nostrils. The narial margins of the anterior leaf are not expanded, and the nostrils are clearly visible. The skull is elongate and comparatively slender, with a low to moderate sagittal crest and uninflated rostral eminences. The zygomata are broad, with a moderate jugal projection. The premaxillae are like those of *H. bicolor* but make a more rounded, less wedge-shaped junction with the maxillae. The palation is more or less V-shaped, with long pterygoids, wide mesopterygoid fossa and a very thin, blade-like projecting vomer. The cochleae are of moderate size, their width a little greater than their distance apart. There is an ovate sphenoidal depression. The anterior upper premolar (pm^2) is minute, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The third upper molar is reduced,

its posterior ridge one quarter or less the length of the anterior ridge. The outer lower incisors are slightly larger in crown area than the inner lower incisors. The anterior lower premolar (pm_2) is much reduced and is from one quarter to one third the length and one quarter to one half the height of the second lower premolar (pm_4). *Hipposideros fulvus* may be distinguished from *H. bicolor* and *H. ater* by its larger ears : from *H. bicolor* by its blade-like vomer and much reduced anterior lower premolar and from *H. ater* by its uninflated internarial septum and broadened zygomata.

DISTRIBUTION : India east to Tonkin and Annam ; Lower Siam.

Hipposideros fulvus fulvus Gray

Hipposideros fulvus Gray, 1838 : 492. Dharwar, India.

Hipposideros murinus Gray, 1838 : 492. Dharwar, India.

Rhinolophus murinus Elliot, 1839 : 99. Dharwar, India. (Re-description of *Hipposideros murinus* Gray, 1838, perhaps based on the same original material.)

Rhinolophus fulgens Elliot, 1839 : 99. Dharwar, India. (Re-description of *Hipposideros fulvus* Gray, 1838, perhaps based on the same original material.)

Phyllorhina aurita Tomes, 1859b : 76. India.

Hipposideros fulvus fulvus occurs in two colour phases : one chestnut brown above and below, the other with the dorsal surface dark brown, the hairs with paler bases and with the ventral surface rather paler than the back. The two colour phases furnish the basis of the names *Hipposideros fulvus* and *Hipposideros murinus* proposed by Gray and likewise of *Rhinolophus fulgens* and *Rhinolophus murinus* proposed by Elliot. This fact was recognized by Wroughton (1912a : 829, 1912b : 1179) who first realized that the descriptions by Elliot most probably related to the bats described by Gray. The type locality of both *Hipposideros fulvus* Gray and *Hipposideros murinus* Gray is given by their describer as Madras. This appears to be an error for Dharwar, whence Elliot obtained the original specimens. Brosset (1962 : 613) has studied the biology of *H. fulvus* and gives measurements and notes on its colour variation.

Tomes in describing *Phyllorhina aurita* failed to compare it in detail with any *Hipposideros* of the *bicolor* type hitherto described from India. His type specimen agrees closely with *H. fulvus*.

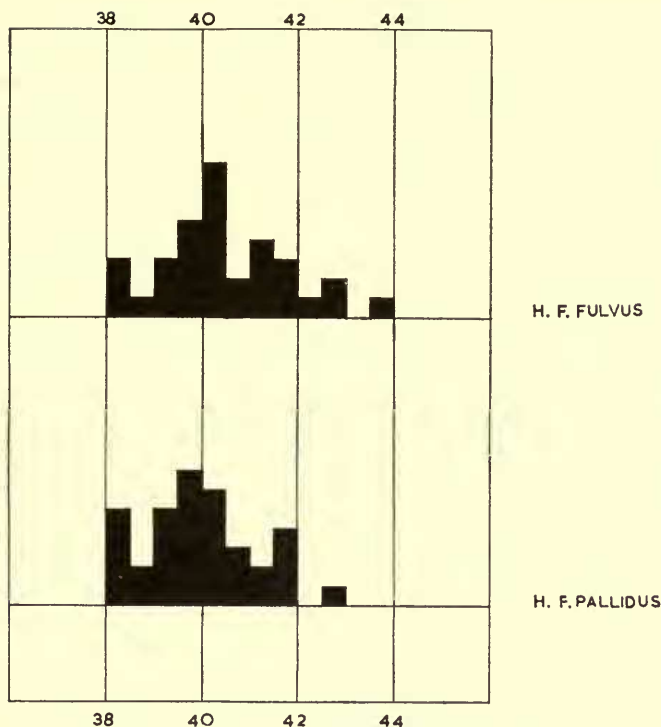
DISTRIBUTION : Ceylon ; Peninsular India (on west coast north to Bombay) ; Bengal, Bhutan Duars ; Sikkim ; Assam ; Burma ; Tenasserim ; Lower Siam ; Tonkin ; Annam.

Hipposideros fulvus pallidus Andersen

Hipposideros fulvus pallidus Andersen, 1918 : 381. Junagadh, Kathiawar, India.

This subspecies differs from *H. f. fulvus* only in its paler back and underparts, the ventral surface being creamy, faintly tinged with grey and lacking all trace of brown.

DISTRIBUTION : Kathiawar ; Gwalior ; Bihar and Orissa ; Sind ; Cutch ; Rajputana ; Baluchistan.

FIG. 6. Length of forearm in *Hipposideros fulvus**Hipposideros cineraceus*

The ears are large and rounded and are similar to those of *H. fulvus*. The noseleaf is similar to that of *H. bicolor*, the internarial septum more or less parallel-sided, inflated and bulbous, with the narial margins of the anterior leaf expanded to partially conceal the nostrils. The skull is comparatively small, with an inflated braincase, low sagittal crest, narrow interorbital region and slightly inflated rostral eminences. The zygomata are narrow and delicate and lack a jugal projection. The premaxillae resemble those of *H. bicolor* and make a wedge-shaped junction with the maxillae. The palation is V-shaped and the mesopterygoid fossa wide, with slightly flared pterygoids. The vomer projects into the mesopterygoid fossa and is thickened posteriorly. The anterior upper premolar (pm^2) is small, compressed between the canine and the second upper premolar (pm^4) but not markedly extruded from the toothrow. The posterior ridge of the third upper molar is one third to one half the length of the anterior ridge. The outer lower incisors are a little larger in crown area than the inner lower incisors. The anterior lower premolar (pm_2) is reduced to a little more than one half the length and height of the second lower premolar (pm_4). The small size of *H. cineraceus* readily distinguishes it from its associated species, except perhaps from *H. ater*: it may be distinguished from this species by its slender, slightly smaller skull, with delicate zygomata which lack a jugal projection, and its

less reduced, unextruded anterior upper premolar. It occurs in two colour phases, the one brownish, the other a brighter, redder phase.

DISTRIBUTION : Northern India west to the Punjab ; Assam ; Burma ; Siam ; Tonkin ; Malay Peninsula ; Riau Archipelago ; Anamba Islands ; Borneo.

***Hipposideros cineraceus cineraceus* Blyth**

Hipposideros cineraceus Blyth, 1853 : 410. Near Pind Dádan Khan, Salt Range, Punjab.

DISTRIBUTION : as above, except perhaps for the foothills of the Himalayas.

***Hipposideros cineraceus micropus* (Peters)**

Phyllorhina micropus Peters, 1872 : 256. Dehra Dun, near Simla, northwestern India.

The type specimen is the only available example of *H. c. micropus*. Its skull is smaller in some respects than the skull of *H. c. cineraceus* and it may represent a northern race.

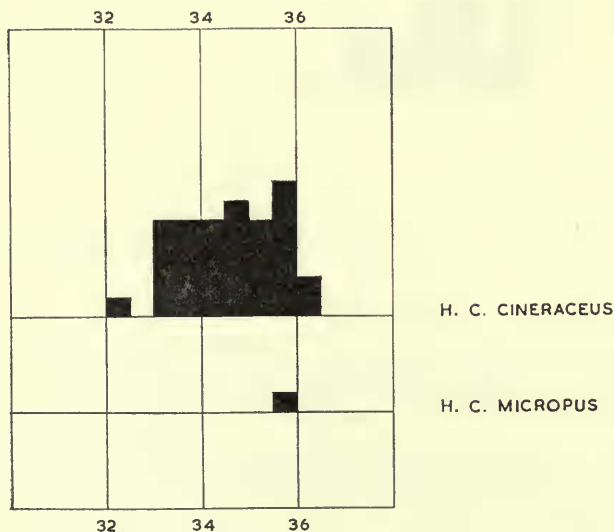


FIG. 7. Length of forearm in *Hipposideros cineraceus*

***Hipposideros nequam* Andersen**

Hipposideros nequam Andersen, 1918 : 381. Klang, Selangor, Federation of Malaya.

The type specimen appears to be the only known example of *H. nequam*. The original description is very brief and no further diagnostic or comparative notes have appeared, although Tate (1941 : 386) noted its relationship to *H. bicolor* and pointed out (p. 362) that its greatly reduced anterior lower premolar (pm_2) separated it from *H. bicolor* with which the length of its forearm would otherwise place it. The ears are large and rounded, similar to those of *H. fulvus*, while the noseleaf is

closely similar to that of *H. bicolor*, but is larger. The internarial septum is uninflated and the narial margins of the anterior leaf are not expanded. The skull of the type specimen is badly damaged and only part of the rostrum with both upper tooththrows and the anterior part of the mandible remain. The rostral eminences are slightly inflated and the anteorbital foramen is large and rather elongate. The premaxillae are short and broad, with delicate enclosing processes which do not encircle the anterior palatal foramina. They make a wedge-shaped junction with the maxillae. The palation is shallowly V-shaped and the mesopterygoid fossa is wide, with a projecting, blade-like vomer. The upper canines have a low posterior cusp, and the anterior upper premolar (pm^2) is small, not extruded from the tooththrow, compressed between the canine and the second upper premolar (pm^4), which has a small anterior cusp. The posterior ridge of the third upper molar is reduced to one half the length of the anterior ridge. The outer lower incisors are very slightly larger in crown area than the inner lower incisors, while the anterior lower premolar (pm_2) is reduced to one half the length and height of the second lower premolar (pm_4). Cranially, *H. nequam* resembles *H. bicolor atrox* and is approximately the same size, but it differs from *H. bicolor* in its slightly more inflated rostral eminences, shorter, broader premaxillae, blade-like vomer and more greatly reduced anterior lower premolar (pm_2). Although the large ears, blade-like vomer and greatly reduced anterior lower premolar (pm_2) suggest a possible relation to *H. fulvus*, *H. nequam* is larger, with a broader rostrum, shorter, much broader premaxillae, which make a wedge-shaped and not rounded junction with the maxillae, wider mesopterygoid fossa and more massive dentition, the canine with a low posterior cusp and the second upper premolar (pm^4) with a small anterior cusp.

Hipposideros calcaratus (Dobson)

Phyllorhina calcarata Dobson, 1877 : 122. Duke of York Island.

The ears of *H. calcaratus* are broad and more or less triangular, their posterior margins with a slight concavity just behind the tip. There is a distinct internal fold. The noseleaf is simple, of medium size, without lateral supplementary leaflets and in general similar to that of *H. bicolor*, with the internarial septum uninflated and the narial margins of the anterior leaf not expanded. The posterior leaf is simple and unwidened, with an ill-defined median supporting septum, the lateral septa weak or absent. A frontal sac is present in both sexes. The skull is unspecialized, very little less elongate than that of *H. bicolor*, with an elongated, uninflated braincase, low sagittal crest, unconstricted interorbital region and slightly inflated rostral eminences. The zygomata are broad, with a well developed jugal projection, the zygomatic width greater than the mastoid width. The premaxillae are elongate and narrow, with delicate anterior enclosing processes which do not encircle the elliptical anterior palatal foramina. They make a U-shaped junction with the maxillae and the palation is shallowly V-shaped, with a wide mesopterygoid fossa and blade-like projecting vomer. The pterygoids are long and

wide and the sphenoidal bridge is wide, partially concealing elongate lateral apertures between pterygoids and alisphenoids. There is a small oval or ovate sphenoidal depression and the width of the cochleae is approximately equal to their distance apart. The mandible is massive, with a substantial coronoid process and a heavy, knob-like angular process. The upper incisors are simple with their outer lobes almost obsolete. The upper canines are massive, with a well developed posterior cusp extending one third or more the length of the tooth. The anterior upper premolar (pm^2) is small, compressed between the canine and the second upper premolar (pm^4), sometimes partially extruded. The third upper molar has its posterior ridge one third or less the length of the anterior ridge. The outer lower incisors are equal in crown area to the inner pair. The anterior lower premolar (pm_2) is only slightly reduced, two thirds or more the length and three quarters the height of the second lower premolar (pm_4).

Tate (1941 : 358, 362) allocated *H. calcaratus* (Dobson) and *H. cupidus* Andersen to a *calcaratus* group distinct from his *bicolor* and *galeritus* groups. There seems to be no justification for this comparatively wide separation : *H. calcaratus* and *H. cupidus* are not greatly removed from *H. bicolor* and its allies and closely resemble them in the basic features of the ears, noseleaf and skull. They differ from *H. bicolor* and its associated species chiefly in their more triangular, less rounded ears, more simplified noseleaves and in having the interorbital region of the skull unconstricted.

DISTRIBUTION : New Guinea ; Bismarck Archipelago : Duke of York Island ; Solomon Islands : Russell ; New Georgia ; Nissan ; Rennell.

***Hipposideros cupidus* Andersen**

Hipposideros cupidus Andersen, 1918 : 383. Eaga, Papua.

The original diagnosis is very brief : Tate (1941 : 362, 381, 382) and Hill (1956 : 77, 78) give supplementary notes. The ears and noseleaf are as in *H. calcaratus*. In its cranial characters *H. cupidus* is closely similar to *H. calcaratus*, but the zygomatics have only a low jugal projection and the pterygoids and sphenoidal bridge are narrow, the sphenoidal bridge not partially concealing wide, rounded lateral apertures. The sphenoidal depression is very poorly developed. The dentition is closely similar to that of *H. calcaratus* but the canines are slender while retaining the high posterior cusp. *Hipposideros cupidus* is in general very similar to *H. calcaratus* and the two species are sympatric for part of their range. Tate (1941 : 362) studied series of both and formulated a key for their separation. Hill (1956 : 77, 78) on the basis of a re-examination of the type specimens commented on the diagnostic characters used by Tate and pointed out that criteria of size do not appear to be valid in the Solomon Islands and that the height of the posterior canine cusp is not a reliable diagnostic character.

DISTRIBUTION : New Guinea ; Japan Island ; Bismarck Archipelago : Duke of York Island ; Tabar Islands ; Solomon Islands : New Georgia ; Banika.

Hipposideros coronatus (Peters)

Phyllorhina coronata Peters, 1871a : 327. Mainit, Surigao, northeastern Mindanao, Philippine Islands.

There is no example of this species in the collections of the British Museum (Natural History). Its size, lack of lateral supplementary leaflets and unspecialized posterior leaf suggests affinity with *H. calcaratus*.

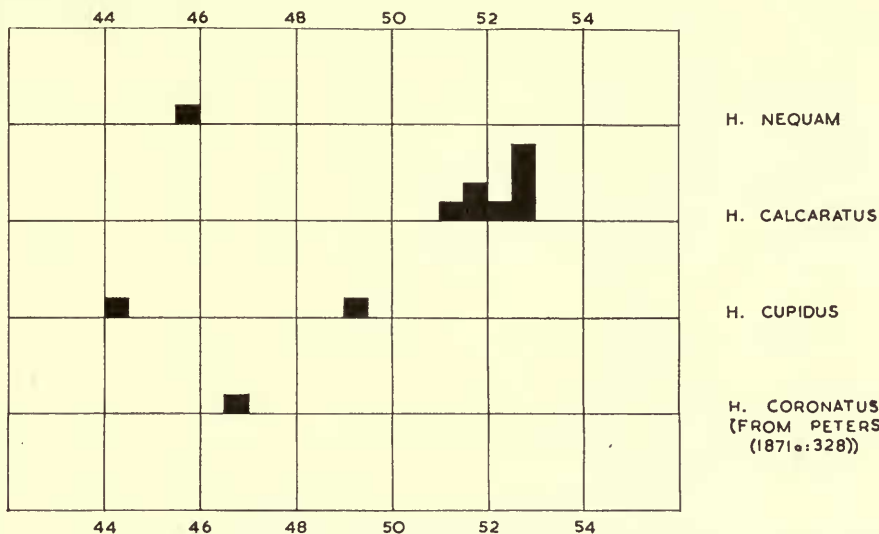


FIG. 8. Length of forearm in *Hipposideros nequam*, *H. calcaratus*, *H. cupidus* and *H. coronatus*

Hipposideros ridleyi Robinson & Kloss

Hipposideros ridleyi Robinson & Kloss, 1911 : 241. Botanic Gardens, Singapore Island.

Gibson-Hill (1949 : 191) believed the type specimen of *H. ridleyi* to be lost. However, in the course of the present study, it was found among a collection of bats sent many years ago to Andersen from the Federated Malay States Museum for study at the British Museum (Natural History). No further specimens appear to have been recorded. The ears are very large and broad, sub-triangular and bluntly pointed, their anterior margins convex, their posterior margins straight for the upper third and not concave. There is a well-developed fold at the antitragal lobe and the ears are haired for their basal quarter. The noseleaf is large, almost completely covering the muzzle and lacks lateral supplementary leaflets. A slight longitudinal swelling behind and parallel to the outer margin of the anterior leaf, however, may represent an incipient leaflet. The anterior leaf is broad, with its narial margins slightly expanded and partially concealing the nostrils. The inter-narial septum is greatly expanded to form a concave circular disc between and anterior to the nostrils which however does not obscure the narial openings. The

narial flaps or lappets are considerably developed to form a pocket encircling the nostrils, but do not rise above the level of the horseshoe. The intermediate part of the leaf is cushion-like, with a low median eminence. The posterior leaf is high, its upper edge semicircular, its lower half supported by three prominent septa of equal depth enclosing four deep pockets, its upper half smooth. The rear walls of the central pockets form a low projecting structure on the posterior face of the leaf. A frontal sac is present in the male type specimen.

The skull is comparatively large and elongate, with broad braincase, low sagittal crest, slight supraorbital ridges, narrow interorbital region, a very shallow frontal depression and slightly inflated rostral eminences. The zygomata are slender with a well developed jugal projection. The anteorbital foramen is elongate, closed by a moderate bar. The premaxillae are short and broad anteriorly, with short anterior enclosing processes. They are narrowed posteriorly to make a wedge-shaped junction with the maxillae and do not enclose the anterior palatal foramina. The palation is U-shaped, with a wide mesopterygoid fossa and a thin, blade-like projecting vomer. The pterygoids are long and wide with a wide sphenoidal bridge, partially concealing elongate lateral apertures. There is an ovate sphenoidal depression and the width of the cochleae is a little greater than their distance apart. The upper incisors are weakly bilobed, their tips strongly convergent and almost touching. The upper canines are slender, with well developed cingula. The anterior upper premolar (pm²) is small, compressed between the canine and the second upper premolar (pm⁴) and the posterior ridge of the third upper molar is one half the length of the anterior ridge. The outer lower incisors are very slightly greater in crown area than the inner lower incisors and the anterior lower premolar (pm₂) is nearly as long as the second lower premolar (pm₄) but only one half its height.

It is evident that *H. ridleyi* is closely related to *H. bicolor* and its immediately associated species, resembling them in having ears with a well developed internal fold, its lack of lateral supplementary leaflets and its narrow, elongate skull with broad brain case and zygomatic width less than the mastoid width. The curious specialization of the internarial septum appears to be a further development of the condition in *H. ater* and *H. cineraceus*, in which the internarial septum, although broadened and bulbous, has not developed an internarial disc or pad, and which tends towards *H. jonesi*, an African species exhibiting a yet more greatly developed internarial disc. This contention is supported by the parallel appearance in *H. ridleyi* of narial pockets and a deeply pocketed posterior leaf, structures found more greatly developed in *H. jonesi*.

Hipposideros jonesi Hayman

[Figure 9]

Hipposideros jonesi Hayman, 1947 : 71. Makeni, Sierra Leone, West Africa.

The ears are very large, broad, sub-triangular, with an acute point, their anterior margins slightly convex, their posterior margins very slightly so, with a faint concavity just behind the tip. There is a distinct internal fold at the antitragal

lobe and the ears are haired for their basal third. The noseleaf is a greatly specialized structure with one well-developed lateral supplementary leaflet extending from the base of the intermediate part of the leaf anteriorly beneath the anterior leaf to the median line, with a deep emargination above the centre of the lip. The anterior leaf is broad, covering almost the entire width of the muzzle, with a faint anterior emargination. The internarial septum is greatly expanded into a large concave, more or less circular disc between and just anterior to the nostrils, which it partially conceals. The narial flaps or lappets form pockets enclosing the nostrils and rise above the level of the anterior leaf. The intermediate part of the leaf is elevated but is otherwise unspecialized. The posterior leaf is high, its outline sub-triangular, with a blunt, rounded point, its lower half supported by a shallow median septum and two deeper lateral septa, forming three deep pockets, the central pocket larger than the lateral pockets and divided by the lower median septum. The posterior walls of the pockets do not form a projecting structure on the posterior face of the leaf and the upper half of the leaf is smooth. The frontal sac is very poorly developed in male specimens and lacking in female examples.

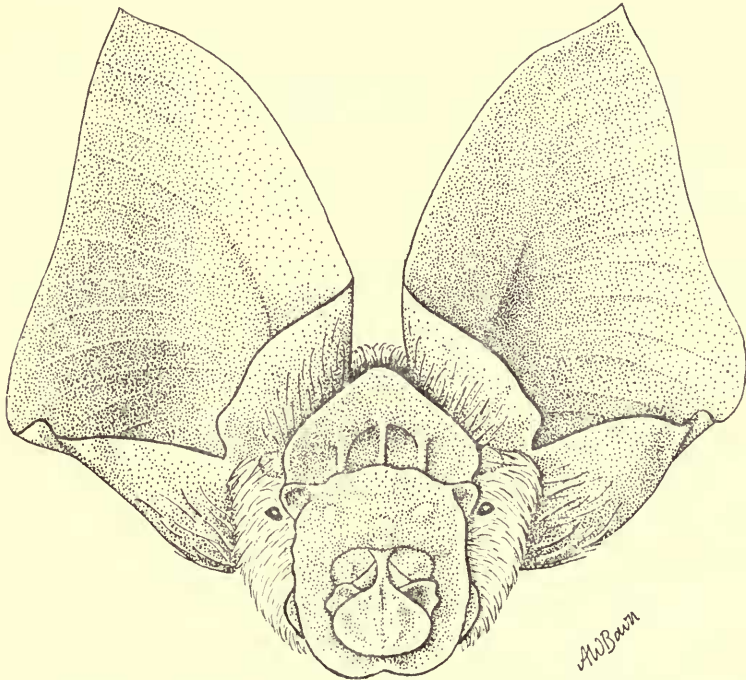


FIG. 9. *Hipposideros jonesi* ♀ (Type B.M. 47.629) (x3)

The skull is of medium size and is elongate with a broad braincase, low sagittal crest, barely definable supraorbital ridges, narrowed interorbital region and rostrum, with a shallow frontal depression and well-inflated rostral eminences. The rostrum is elongate, the premaxillae projecting beyond the canines. The zygomata are

slender, with a low jugal process, and the zygomatic width is considerably less than the mastoid width. The anteorbital foramen is rounded and closed by a narrow bar. The premaxillae are broad anteriorly with delicate anterior enclosing processes: they are narrowed posteriorly and do not enclose the large rounded anterior palatal foramina, making a V-shaped junction with the maxillae. The palation is square, with a post-palatal spicule. The mesopterygoid fossa is wide, with a blade-like, projecting vomer. The pterygoids are long and flaring, partially concealing large lateral apertures, although the sphenoidal bridge is narrow. There is a shallow sphenoidal depression. The cochleae are large, their width equal to two times or a little more their distance apart, with a rather narrow basioccipital. The upper incisors lack the outer lobe, and although convergent their tips are widely separated. The upper canines have weak anterior and posterior cusps. The anterior upper premolar (pm^2) is of moderate size, slightly extruded and compressed between the canine and the second upper premolar (pm^4). The posterior ridge of the third upper molar is one half or slightly less the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than that of the inner lower incisors and the anterior lower premolar (pm_2) is equal approximately to one half the length and height of the second lower premolar (pm_4).

Hayman (1947 : 73) pointed out that *H. jonesi* stood apart from any of the groups defined and keyed by Tate (1941), noting that while in size, the form of the ears and in the mastoid width exceeding the zygomatic width it approached the *bicolor* group of species as understood by Tate, in other features such as the well-developed single supplementary leaflet and the absence of a frontal sac it differed widely from this and the other groups of the genus. Later, Aellen (1954 : 480) keyed and listed *H. jonesi* as the sole species of a *jonesi* group. However, there seems little doubt that *H. jonesi* should be allocated to the group of species typified by *H. bicolor* and its allies. As in these species, the ears have a distinct internal fold and are haired for one third of their length. The skull has the elongate outline typical of *H. bicolor* and its associated species, with a similarly broad braincase. The nearest ally to *H. jonesi* appears to be *H. ridleyi*, a Malaysian species exhibiting similar specialization of the noseleaf, although as might be expected from the wide geographical separation of the two species, there are very considerable differences between them. Both have large, sub-triangular ears with a well-defined internal fold: their noseleaves are wide, covering the muzzle almost entirely: in each the internarial septum is expanded to form a disc-like structure and circumnarial pockets have been developed while both have a high posterior leaf, its lower half deeply pocketed and its upper half smooth. *Hipposideros jonesi* differs markedly from *H. ridleyi* in the possession of a well-developed lateral supplementary leaflet which in *H. ridleyi* is merely incipient: the internarial disc in *H. jonesi* is larger and the posterior leaf more developed, with its upper edge triangular in outline and not rounded as in *H. ridleyi*. Cranially, the two species are closely similar and have skulls essentially resembling those of *H. bicolor* and its immediate allies: *H. jonesi* has a smaller, more slender skull than *H. ridleyi* with a square and not U-shaped palation and larger cochleae, with narrowed basioccipital and sphenoidal bridge. Their dentition

differs principally in that the upper incisors of *H. jonesi* are placed at the outer margins of the premaxillae and although convergent have their tips separated : those of *H. ridleyi* are more medially sited and have their tips strongly convergent and almost touching. *Hipposideros jonesi* is the most specialized species of the more primitive *bicolor* section of the *bicolor* group, retaining the more or less rounded ears, elongate rostrum and narrowed zygomata of the *bicolor* type and yet with a greatly specialized noseleaf associated with some specialization of the auditory region of the skull. Together with the similar but less specialized species *H. ridleyi* it constitutes an offshoot of the *bicolor* type leading apparently to no further specialization. Its differences from the Malaysian *H. ridleyi* are of a considerable order of magnitude and indicate remote separation of the parental stems.

DISTRIBUTION : West Africa : Sierra Leone ; Guinea (for notes on specimens from Guinea see Eisentraut & Knorr (1957 : 333)).

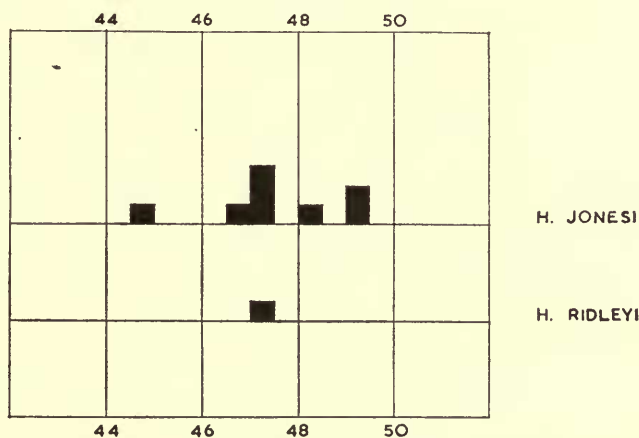


FIG. 10. Length of forearm in *Hipposideros jonesi* and *H. ridleyi*

Hipposideros dyacorum Thomas

Hipposideros dyacorum Thomas, 1902 : 271. Mount Mulu, Baram, Sarawak, Borneo.

The ears are of moderate size, broad at the base, sub-triangular, their anterior margins convex, their posterior margins with a slight concavity just behind the tip but otherwise convex. There is a well-defined internal fold at the antitragal lobe and the ears are sparsely haired for about one half of their length. The noseleaf is small, narrow and simple, and lacks lateral supplementary leaflets. It is very like the noseleaf of *H. bicolor*, with the internarial septum slightly inflated, triangular, broad at its base, narrowed between the nostrils and with the narial margins of the anterior leaf slightly expanded but not concealing the nostrils. The intermediate part of the leaf is cushion-like, with a low, slightly inflated median eminence. The posterior leaf is thin, its upper edge semicircular, and is supported by a well-defined median septum and two less prominent lateral septa. There is a small frontal sac in the female type specimen.

The skull is short and the braincase strongly inflated with a low sagittal crest. The interorbital region is constricted and the supraorbital ridges, although low, are sharply defined and prominent. There is a shallow frontal depression and the rostrum is slightly broadened, with moderately inflated rostral eminences. The zygomata are slender with a moderate jugal projection, and the anteorbital foramen is elongate, closed by a very slender bar. The premaxillae are entirely fused, their junction with the maxillae shallowly V-shaped, the maxillae with an abrupt emargination at the apex of the V. The enclosing processes of the premaxillae are delicate and hook-shaped, but do not enclose the rounded anterior palatal foramina. The palation is U-shaped, with an abrupt median emargination. The vomer does not project into the mesopterygoid fossa, which is not greatly widened. The pterygoids are long, the pterygoid wings flaring, together with the slightly constricted sphenoidal bridge partially concealing elongate lateral apertures. There is a shallow sphenoidal depression. The width of the cochleae is equal to their distance apart. The upper incisors are very weakly bilobed, and the upper canines have weak anterior and posterior cusps. The anterior upper premolar (pm²) is minute, extruded, with the canine and the second upper premolar (pm⁴) in contact. The posterior ridge of the third upper molar is obsolete. The crown area of the outer lower incisors is very slightly greater than that of the inner lower incisors. The anterior lower premolar (pm₂) is much reduced, to one quarter the length and height of the second lower premolar (pm₄). Measurements of specimens of *H. dyacorum* from southwestern Borneo are given by Lyon (1911 : 129, 130) while a description, with measurements, of a series from North Borneo is provided by Davis (1962 : 39).

Hipposideros dyacorum forms a link between *H. bicolor* and *H. galeritus*, and although independently slightly specialized in some respects displays some characters indicative of the aggregations of species to which they belong. The ears and nose-leaf of *H. dyacorum* correspond closely to those of *H. bicolor* and its allies, while its skull is shortened like that of *H. galeritus* and its associated species, and has the long pterygoids common to both aggregations of species. The dentition of *H. dyacorum* is more advanced than that of *H. bicolor* and its allies and in the reduction of the premolars tends towards *H. galeritus*.

DISTRIBUTION : Borneo.

Hipposideros sabanus Thomas

Hipposideros sabanus Thomas, 1898 : 243. Lawas, North Borneo.

The ears are large and broad, rounded and not acutely pointed, their posterior margins evenly convex. They are thickened at the antitragal lobe but lack a definite internal fold, and are haired for the basal third of their length. The noseleaf is small and comparatively simple, lacking lateral supplementary leaflets. The anterior leaf is narrow, with a well-defined median emargination. The internarial septum is swollen and bulbous, especially posteriorly, but does not conceal the narial apertures, which are flanked by small narial lappets. The intermediate part

of the leaf is cushion-like but not greatly inflated. The posterior leaf is high, without supporting septa and has a semicircular upper edge. It is specialized by the development from its posterior face of a transverse supplementary structure, with a slightly serrate upper edge below that of the posterior leaf. There is a small frontal sac in the female type specimen.

The skull is small, with a broad braincase and low sagittal crest. The interorbital region is moderately constricted while the supraorbital ridges are not sharply defined and are very weak. There is no frontal depression, the rostrum in profile exhibiting a slight convexity. The rostrum is short and not broadened, the rostral eminences only slightly inflated. The zygomata are slender with a high jugal process, their combined width greater than the mastoid width. The anteorbital foramen is elongate, closed by a very slender bar. The premaxillae are short and broad, their junction with the maxillae V-shaped, while the anterior palatal foramina are rounded and enclosed within the premaxillae by a narrow bar. The palation is only slightly rounded, almost square, without a median emargination. The mesopterygoid fossa is wide, with a slightly projecting vomer, while the pterygoids are short and the sphenoidal bridge narrow, exposing large rounded lateral apertures. There is a shallow sphenoidal depression and the cochleae in width slightly exceed their distance apart. The upper incisors are not bilobed, the outer lobe obsolete, while the upper canines have a weak anterior cusp and a trace of the posterior cusp. The anterior upper premolar (pm^2) is obsolete, the second upper premolar (pm^4) with a low anterior cusp in contact with the canine. The posterior ridge of the third upper molar is reduced to one third the length of the anterior ridge. The crown area of the outer lower incisors is very slightly greater than that of the inner lower incisors, while the anterior lower premolar (pm_2) is much reduced, one quarter the length and height of the second lower premolar (pm_4) and is slightly extruded from the toothrow.

The collections of the British Museum (Natural History) contain a specimen from Sumatra (B.M. 27.5.9.3) which hitherto has been referred to *H. doriae* (Peters). However, its ears agree exactly with those of *H. sabanus*, and although the noseleaf has been partially destroyed, sufficient remains intact to show that the posterior leaf lacks supporting septa and has the low transverse serrated supplementary structure typical of *H. sabanus* developed from its posterior face. Cranially, this specimen agrees very closely with *H. sabanus* but has the sphenoidal depression a little more sharply defined and the upper incisors weakly bilobed, the outer lobe obsolescent. In view of these considerations it is referred to *H. sabanus*, which Chasen (1940 : 481) had already recorded from Sumatra.

I am unable to agree with Tate (1941 : 366, 383, 388) that *H. dyacorum* and *H. sabanus* are closely related or even allied. At most they appear to share a common origin among the more primitive bats of the *bicolor* subgroup to which they both display affinity, but otherwise they appear to represent two differing and widely divergent lines of development. Although *H. dyacorum* has more or less triangular ears with a slight posterior concavity, its ears nevertheless have a well-defined internal fold and its noseleaf is simple, lacking lateral supplementary leaflets.

Hipposideros sabanus has the broad, rounded ears characteristic of the *bicolor* subgroup, with convex posterior edges but without an evident internal fold. Its noseleaf, although rather small, without lateral supplementary leaflets and basically of the *bicolor* type, is more specialized, with the posterior leaf lacking supporting septa and with a transverse supplementary structure on its posterior face. The two species differ sharply in their cranial characters. *Hipposideros dyacorum* has a longer skull than *H. sabanus*, and has a wider rostrum with the rostral eminences more inflated. The palate in *H. dyacorum* is very much longer and the palation U-shaped and not square : its pterygoids are long and the sphenoidal bridge is wide, in contrast to *H. sabanus*, which has short pterygoids and a narrow sphenoidal bridge. The anterior lacerated foramina of *H. dyacorum* are elongate and narrow, while those of *H. sabanus* are rounded and wide. These differences in cranial architecture indicate considerable separation, and the two species do not appear to be closely related.

Hipposideros dyacorum appears to be more closely related to *H. bicolor* and its immediate allies than does *H. sabanus*. Its ears retain the internal fold : its noseleaf is largely unspecialized and the skull is slightly elongate, the palate not extensively shortened. Its long pterygoids and wide sphenoidal bridge suggest relationship with *H. galeritus* and its associated species and it is clearly derived from the line connecting them to the less specialized species associated with *H. bicolor*. *Hipposideros sabanus*, although with ears of the *bicolor* type, has a more advanced noseleaf and a shorter, less elongate skull. Its much shorter palate indicates closer relationship to the *galeritus* subgroup than is evident in *H. dyacorum* : the features of its posterior leaf, which lacks supporting septa and which has a low posterior transverse structure, together with the short pterygoids and narrow sphenoidal bridge suggest that it has been derived from the stem leading to *H. caffer* and its allies.

DISTRIBUTION : Borneo ; Sumatra.

Hipposideros doriae (Peters)

Phyllorhina doriae Peters, 1871a : 326. Sarawak, Borneo.

The collections of the British Museum (Natural History) contain no specimen referable to *H. doriae* and it has not been possible to examine the type specimen, described by Peters from the collections of the Marquis J. Doria and apparently deposited in the collections of the Museo Civico di Storia Naturale at Genoa. Although Peters described only the external features of *H. doriae* there seems little doubt from his description that it belongs to that section of the genus typified by *H. bicolor* and is very similar, if not identical to *H. sabanus*. The ears lack a distinct tip and have their anterior and posterior margins equally convex for their terminal third. The noseleaf lacks supplementary lateral leaflets and the posterior leaf has a smooth anterior face, without supporting septa. There is a small but distinct frontal sac. Further notes on the type specimen were obtained by Oldfield Thomas from R. Gestro of the Museo Civico di Storia Naturale and are preserved in the archives of the British Museum (Natural History) for 1902. They have also been

recorded by Thomas as a marginal note to the account of *H. doriae* (p. 146) in a copy of Dobson, 1878, Catalogue of the Chiroptera in the collection of the British Museum, now in the library of the British Museum (Natural History). The features of the type specimen noted by Gestro are that the anterior leaf has no median emargination : that the anterior upper premolar (pm_2) is absent and that the anterior lower premolar (pm_3) is small, a diagram drawn by Gestro suggesting that it is less than one half of the size of the second lower premolar (pm_4). Thomas adds in his marginal note that *H. sabanus* is probably equal to *H. doriae* : the close agreement of noseleaf and dentition suggests that *H. doriae* is related to *H. sabanus* rather than to *H. bicolor* as was suggested by Dobson (1878 : 147) and Tate (1941 : 383). The two species are clearly very similar and seem likely to be at least conspecific, in which case it should be noted that *doriae* is the prior name by many years.

Hipposideros obscurus (Peters)

Phyllorhina obscura Peters, 1861 : 709. Paracali, Luzon, Philippine Islands.

The following notes are based on a small series (B.M. 77.10.6.14-18) in the collections of the British Museum (Natural History), from Dinagat Island, Philippine Islands, consisting of an adult male and female, together with three young males. The ears are sharply triangular, broad at the base, their anterior margins markedly convex and their posterior margins with a concavity just behind the acute point. There is no internal fold but the ear membrane is thickened at the antitragal lobe and there is a small antitragal projection. The ears are haired for one half of their length. The noseleaf is of moderate size and does not entirely cover the muzzle : it lacks lateral supplementary leaflets but has a distinct raised glandular ridge directly beneath the edge of the anterior leaf, extending laterally under the margins of the anterior leaf and anteriorly beneath this leaf to the median line. The anterior leaf in the adult male has a small but distinct median emargination which in the adult female is very small : it is present but very small in two of the young male specimens and absent in the third. The internarial septum is not inflated and is broadly triangular, narrow between the nostrils, which lie at the base of a deep depression : the narial lappets are moderately developed and the narial margins of the anterior leaf are slightly expanded. The intermediate part of the leaf is cushion-like, slightly inflated, with a low median ridge or eminence. The posterior leaf is high, its upper edge semicircular and lacks supporting septa, with a low transverse ridge on its posterior face. There is a well-developed frontal sac in the male, represented by a depression in the female specimen.

The skull is short and comparatively broad, with a broad, inflated braincase, low sagittal crest and a moderately constricted interorbital region. There is no frontal depression and the rostrum is broad and rounded, with slightly inflated rostral eminences. The zygomata are slender, their combined width a little greater than the mastoid width. The anteorbital foramen is large and elongate, closed by a narrow bar. The junction of the premaxillae with the maxillae is shallowly V-shaped and the palate is short : the palation is U-shaped with a small post-palatal spicule.

The mesopterygoid fossa is wide, the vomer not projecting and the pterygoids long, together with the moderate sphenoidal bridge partially concealing wide lateral apertures. There is a small sphenoidal depression and the width of the cochleae is equal to their distance apart. The anterior upper premolar (pm^2) is small and is extruded into the angle between the canine and the second upper premolar (pm^4), which however are not in contact, while the posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is slightly greater than that of the inner pair. The anterior lower premolar (pm_2) is three quarters the length and height of the second lower premolar (pm_4).

Hipposideros obscurus is the last species of the *bicolor* type and like *H. dyacorum*, apparently links the more primitive of these to *galeritus* and its allies, although it has no apparent close connection with *H. dyacorum* and in some respects inclines towards *H. sabanus*. Its ears are very like those of *H. dyacorum* but lack the internal fold while its noseleaf, although of *bicolor* type, has deeply depressed nostrils suggestive of *H. pygmaeus* or *H. coxi*, and a posterior leaf lacking septa and with a posterior transverse structure reminiscent of *H. sabanus*. The short, broad skull has the long pterygoids characteristic of *H. galeritus* and its associates as distinct from *H. caffer* and its allies but the dentition, retaining the anterior upper premolar, is less advanced than in *H. dyacorum* and *H. sabanus*.

DISTRIBUTION : Philippine Islands : Luzon ; Dinagat ; Mindanao (Sanborn (1952 : 104)).

Hipposideros marisae Aellen

Hipposideros marisae Aellen, 1954 : 474, fig. 1. White Panther Rock, Duékoué, Ivory Coast.

No example of *H. marisae* has been examined, and the following notes have been compiled from the original description. The ears are large, broad and bluntly pointed, with a concavity behind the tip. There is no antitragal fold. The nose-leaf is small with one very small lateral supplementary leaflet. The anterior leaf has apparently no median emargination and the internarial septum is inflated, slightly disc-like between the nostrils. The intermediate part of the leaf is slightly inflated while the posterior leaf is high, its upper edge semicircular, and is supported by three septa enclosing deep pockets. A frontal sac is present in the male type specimen.

The skull is said to be in general similar to that of *H. bicolor* and *H. curtus*, with a weak sagittal crest, narrow rostrum, comparatively wide zygomata, their combined width greater than the mastoid width, and small bullae. The dentition is apparently similar to that of *H. curtus* : the upper incisors lack the outer lobe and the anterior upper premolar (pm^2) is small and slightly extruded while the anterior lower premolar (pm_2) is one half the height of the second lower premolar (pm_4).

Aellen (1954 : 474 et seq.) has considered the taxonomic status of *H. marisae* and its relative *H. curtus* in some detail, and concluded that neither are closely related to *H. caffer* and its immediate allies but to the *bicolor* group (the *bicolor* subgroup as here understood). Aellen further proposed that *H. marisae* and *H. curtus* should be considered to represent a group within *Hipposideros*, the *curtus*

group, characterized by large emarginated ears lacking an internal fold, one or two lateral supplementary leaflets, swollen claviform internarial septum, the presence of a frontal sac in males, sometimes absent in females, the fourth metacarpal longer than the third and fifth and by a small, slightly extruded anterior upper premolar (pm^2). However, there seems no justification for this action. *Hipposideros curtus*, with ears and noseleaf similar to those of the *bicolor* subgroup yet with two lateral supplementary leaflets and skull tending towards the *galeritus* subgroup, particularly towards *H. caffer*, is clearly derived from the *bicolor-caffer* stem. Similarly, another such derivative, *H. fuliginosus*, which Aellen places in a *caffer* group, has ears and noseleaf closely similar to those of *H. caffer*, yet has a skull exhibiting a number of the features of the *bicolor* subgroup. From the original description, *H. marisae* presents yet a further combination of characters, having slightly specialized ears lacking an internal fold but otherwise like those of the *bicolor* subgroup and in the possession of a simple noseleaf similar to that of *H. bicolor*, with one small, rudimentary lateral supplementary leaflet. Its skull appears to be similar to the skulls of the members of the *bicolor* subgroup, rather elongate and narrow, with the zygomatic width only barely exceeding the mastoid width. It too represents the *bicolor-caffer* stem, and is a less advanced species than either *H. curtus* or *H. fuliginosus*.

Hipposideros marisae, *H. curtus* and *H. fuliginosus* form connecting links between *H. bicolor* and its associated species and the more specialized *H. caffer*. As is not unusual in the genus, specialization of the various species has reached different levels: *H. marisae* and *H. curtus* have ears and noseleaves rather of the pattern of *H. bicolor*, modified by the presence of one lateral supplementary leaflet in *H. marisae* and the presence of two such leaflets in *H. curtus*, while *H. marisae* has a skull of the *bicolor* type and *H. curtus* a skull tending towards *H. caffer*. *Hipposideros fuliginosus* has *caffer*-like ears and noseleaf associated with a skull similar to that of the members of the *bicolor* subgroup. The characters of its ears and noseleaf ally it more closely to *H. caffer* than to *H. marisae* and *H. curtus* and it is less closely related to these species than they are to each other. Both are characterized by a swollen, claviform internarial septum which tends to form a disc-like structure between the nostrils, a specialization found in far more greatly developed form in *H. ridleyi* and *H. jonesi*, two species forming a development of *H. bicolor* and its allies. For this reason, *H. marisae* and *H. curtus* are considered to form an independent offshoot of the *bicolor-caffer* stem. There seems little point in constructing groups for intermediate species, based largely on the characters that they share in common with the species they link together, and the *curtus* group of Aellen (1954 : 479) in the present work is considered to form a part of the *bicolor* group as here understood.

Hipposideros pygmaeus (Waterhouse)

Rhinolophus pygmaeus Waterhouse, 1843 : 67. Philippine Islands.

The type specimen is the only available example of *H. pygmaeus*. It is a very small bat with the ears sub-triangular, very broad at the base, pointed, with the

upper portion of their anterior margins very slightly concave and their posterior margins concave behind the tip. The ears are slightly thickened at the antitragal lobe and are haired for one half of their length. The noseleaf is large, entirely covering the muzzle, and has two lateral supplementary leaflets, the anterior leaflet extending from the base of the intermediate part of the leaf forward beneath the anterior leaf to the median line but with a median emargination, the posterior leaflet well developed and extending slightly anteriorly. The internarial septum is very small and reduced, insignificant between the nostrils: the narial lappets are greatly developed, especially laterally, and rise above the level of the horseshoe. They are elongated and almost completely encircle the nostrils, which lie at the base of the small pockets so formed. The intermediate part of the leaf is well inflated but lacks eminences. The posterior leaf is high, thin, its upper edge semicircular, and is supported by three well-defined septa which enclose four small but moderately deep pockets. There is no frontal sac in the female type specimen: according to Tate (1941: 369) it is present in males.

A small anterior portion of the skull is all that remains. The sagittal crest, represented by a remnant, is evidently low and the interorbital region is constricted, but not sharply so, with no evident supraorbital ridges. There is no frontal depression. The rostrum is slightly shortened, high and rounded, the rostral eminences well inflated with a slight median depression between them. The anteorbital foramen is large and rounded, closed by a very narrow bar. The upper incisors are weakly bilobed, the outer lobe obsolescent. The upper canines have a moderate anterior cusp and a stronger posterior cusp extending for about one third of the length of the tooth. The anterior upper premolar (pm^2) is small but is barely out of alignment in the toothrow, separating the canine and the second upper premolar (pm^4), which has a distinct anterior cusp. The posterior ridge of the third upper molar is one half of the length of the anterior ridge.

Tate (1941: 367, 369, 388) considered *H. pygmaeus* to be an isolated species derived from the line leading to *H. galeritus* and its allies. This view appears to be correct, and despite its extended anterior lateral supplementary leaflets and inflated rostral eminences which suggest relationship to *H. coxi*, its affinities lie more closely with *H. galeritus* and its associated species. Although the anterior lateral supplementary leaflets in *H. pygmaeus* extend anteriorly beneath the anterior leaf to the median line as in *H. coxi*, the two species differ sharply in that the leaflets in *H. pygmaeus* are not continuous over the upper lip as in *H. coxi*, but are divided to the base by a sharp median emargination. This condition suggests *H. galeritus*, in which the leaflets, although extending forward beneath the anterior leaf, do not reach the median line. The narial part of the noseleaf in *H. pygmaeus* is slightly more specialized than that of *H. obscurus*, also a derivative of the *galeritus* stem. The posterior leaf is divided by blade-like septa as in *H. galeritus*, and its margins at the base display none of the extraordinary complexity of *H. coxi*. The skull is not excessively shortened and the dentition not greatly specialized, providing a link with the *bicolor* type of skull. Vertical inflation of the rostral eminences appears to be a correlation of increasing complexity of the narial region of the noseleaf. *Hippo-*

sideros obscurus, in which the narial apertures are situated at the base of a deep depression but are not noticeably pocketed, has slightly inflated rostral eminences. In *H. pygmaeus* the narial region is slightly more specialized: the narial lappets are elongated to form small pockets almost completely encircling the nostrils and the rostral eminences are well inflated. *Hipposideros coxi* has the narial apertures completely concealed within a pocket formed by the narial lappets and the inter-narial septum: correspondingly the rostral eminences are much inflated and appear as two separate raised structures. On the balance of characters, therefore, *H. pygmaeus* is associated with *H. galeritus* and its allies.

DISTRIBUTION: Philippine Islands: Luzon; Negros (Sanborn (1952: 104)).

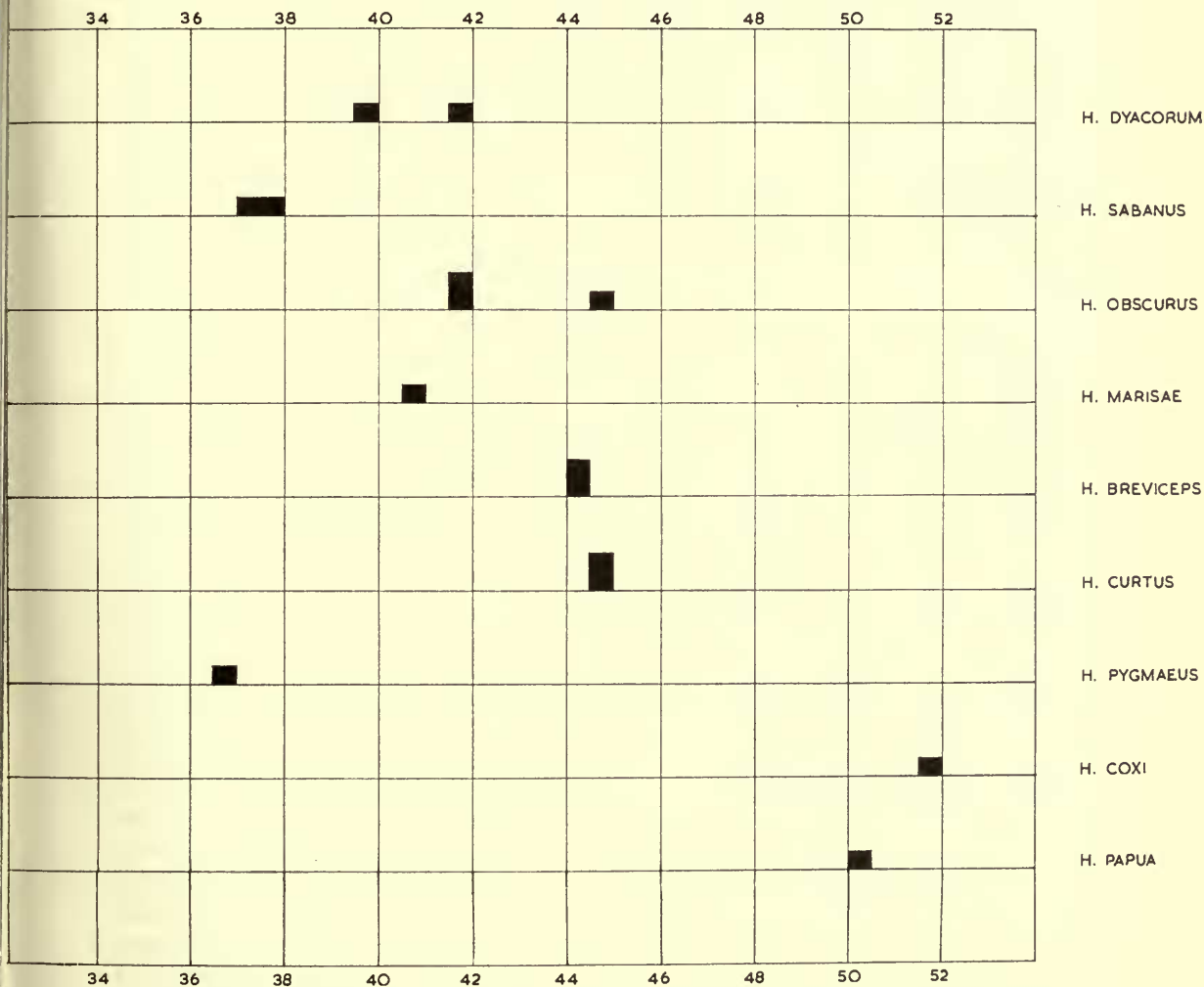


FIG. 11. Length of forearm in *Hipposideros dyacorum*, *H. sabanus*, *H. obscurus*, *H. marisae*, *H. breviceps*, *H. curtus*, *H. pygmaeus*, *H. coxi* and *H. papua*

Hipposideros galeritus

The ears are broad, triangular and acutely pointed, their anterior margins convex, their posterior margins concave behind the tip but otherwise convex, without a marked antitragal fold but thickened at the antitragal lobe, with a small antitragal projection. They are haired for three quarters of their length. The noseleaf is small and comparatively simple, with two well-developed lateral supplementary leaflets, which project beyond the lateral margins of the anterior leaf. The anterior lateral supplementary leaflet extends from the base of the posterior leaf anteriorly beneath the anterior leaf on to the upper lip but does not reach the median line. This condition is similar to that found in *H. pygmaeus*, in which the anterior leaflets on each side do in fact extend anteriorly to the median line, but are separated by a deep emargination above the centre of the upper lip. The posterior lateral supplementary leaflet is broad but is shorter than the anterior leaflet, only just extending on to the upper lip. The anterior leaf is not emarginated. The internarial septum is more or less parallel-sided and is not inflated: the narial lappets are well developed and project slightly above the level of the anterior leaf. Although lying in a depression, the nostrils are not enclosed by narial pockets. The intermediate part of the leaf is slightly inflated and cushion-like but has no swollen prominences. The posterior leaf is thin, its upper edge semicircular with no trace of lobulation, and is supported by three well-defined septa enclosing four small pockets. There is a frontal sac in males, represented in female specimens by a depression containing a tuft of hairs.

The skull is short and broad, with an inflated, almost globose braincase and a low to moderate sagittal crest. The interorbital region is constricted, with sharply defined supraorbital ridges. There is a shallow frontal depression and the rostral eminences are moderately inflated, separated by a shallow groove. The zygomata are slender, with a low to moderate jugal projection, the zygomatic width exceeding the mastoid width. The postorbital processes are incipient, giving the rostrum from above a slightly pentagonal aspect. The anteorbital foramen is elongate and closed by a narrow bar. The premaxillae are fused for their entire length, their junction with the maxillae shallowly V-shaped. Their anterior enclosing processes are slender and do not entirely enclose the more or less oval anterior palatal foramina. The palate is short and broad, the palation U-shaped with usually a small median post-palatal spicule. The mesopterygoid fossa is wide, the vomer not projecting or projecting only slightly, the pterygoids elongated, with the wide sphenoidal bridge partially concealing elongate lateral apertures. There is a well-defined sphenoidal depression, while the width of the cochleae is a little greater than their distance apart. The upper incisors are not bilobed or are only very weakly bilobed, with only a trace of the external lobe. The upper canines have a moderate anterior cusp and a well developed posterior cusp, both low. The anterior upper premolar (pm²) is usually much reduced, minute, extruded from the toothrow, the canine and the second upper premolar (pm⁴) in contact or nearly so. The posterior ridge of the third upper molar is reduced to one third of the length of the anterior ridge. The crown area of the outer lower incisors is about the same or very slightly greater

than that of the inner pair. The anterior lower premolar (pm_2) is usually reduced to one half or less of the length and height of the second lower premolar (pm_4).

DISTRIBUTION : India ; Malay Peninsula east to Solomon Islands and New Hebrides ; northern Australia.

Hipposideros galeritus galeritus Cantor

Hipposideros galeritus Cantor, 1846 : 183. Penang.

Tate (1941 : 367) has thrown considerable doubt on the authenticity of the skull of the type specimen of *Hipposideros galeritus* Cantor and has suggested that the skin and skull may be mismatched. The type specimen is now B.M. 79.11.21.85 in the collections of the British Museum (Natural History), a skin and skull, labelled as a male. In the register of the mammal collections in the British Museum (Natural History) for 1879, the specimen is listed as a skin only, with no mention of a skull. The skin is preserved in the dry state and fortunately is in good condition. The ears are broad at the base, triangular and sharply pointed, their posterior margins with a concavity just behind the tip. The noseleaf has two lateral supplementary leaflets and the posterior leaf is thin, supported by three septa. The skull associated with this skin is small, rather elongate, with a low sagittal crest, constricted inter-orbital region, no supraorbital ridges and moderately inflated rostral eminences. The zygomata are slender, with a well-developed superior projection, the zygomatic width (by extrapolation) less than the mastoid width. The anteorbital foramen is slightly elongate, closed by a narrow bar. The junction of the premaxillae with the maxillae is acutely V-shaped. The palation is U-shaped, with the vomer projecting very slightly into the mesopterygoid fossa. The sphenoidal bridge is moderate, not concealing the lateral apertures. There is a shallow sphenoidal depression. The upper incisors are weakly bilobed and the upper canines are slender, with a low posterior cusp. The anterior upper premolar (pm^2) is minute, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact. The posterior ridge of the third upper molar is one half the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than that of the inner pair and the anterior lower premolar (pm_2) is two thirds the length and one half the height of the second lower premolar (pm_4). It is clearly the skull of a member of the *bicolor* subgroup and agrees closely with *H. ater*. It is therefore necessary to adopt the suggestion by Tate that *Hipposideros galeritus* Cantor be restricted to the skin of the type specimen, disregarding the skull hitherto associated with that skin.

The characters of *H. g. galeritus* are much as in the species diagnosis. The upper incisors are not bilobed, the outer lobe being obsolete. The anterior upper premolar (pm^2) is very small, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact. The anterior lower premolar (pm_2) is one third to one half the length and height of the second lower premolar (pm_4). Davis (1961 : 90) gives a description, with measurements, of a series of *H. g. galeritus* from the Federation of Malaya.

DISTRIBUTION : Malay Peninsula ; Riau Archipelago ; Banka Island ; South Natuna Islands.

***Hipposideros galeritus brachyotus* (Dobson)**

Phyllorhina brachyota Dobson, 1874b : 237. Central India.

The characters of this subspecies are largely those of the nominate subspecies, but the post-palatal spicule is usually very small or absent, and the dentition is less advanced. The anterior upper premolar (pm^2), although small, is not always completely extruded from the toothrow but is compressed tightly between the outer margins of the canine and the second upper premolar (pm^4), while in some specimens it is extruded from the toothrow with the canine and the second upper premolar in contact. The posterior ridge of the third upper molar is one half the length of the anterior ridge. The anterior lower premolar (pm_2) is less reduced than in *H. g. galeritus*, and is nearly as long as the second lower premolar (pm_4) and two thirds its height. Brosset (1962 : 618) has studied the biology of *H. galeritus* in India, and gives measurements and notes on its colour variation.

DISTRIBUTION : Ceylon ; India : Mysore ; Bombay ; Bengal.

***Hipposideros galeritus schneideri* Thomas**

Hipposideros schneideri Thomas (misprint), 1904b : 722. Upper Langkat, Sumatra.

The posterior leaf is supported by a prominent median septum, the lateral septa not greatly developed and represented by low ridges. The post palatal spicule is absent. The upper canines have a low anterior cusp, their posterior cusp insignificant or low. The anterior upper premolar (pm^2) is minute or lacking (it is absent in one side of the jaw of the type specimen, vestigial in the other side) the canine and the second upper premolar (pm^4) in contact. The anterior lower premolar (pm_2) is much reduced and is one third to one half the length and height of the second lower premolar (pm_4). Tate (1941 : 367) suggests that *H. g. schneideri* is a derived species of *H. galeritus*. There seems no reason, however, to separate it from this species with which it shares a majority of characters, differing principally in the greater reduction of the anterior premolars.

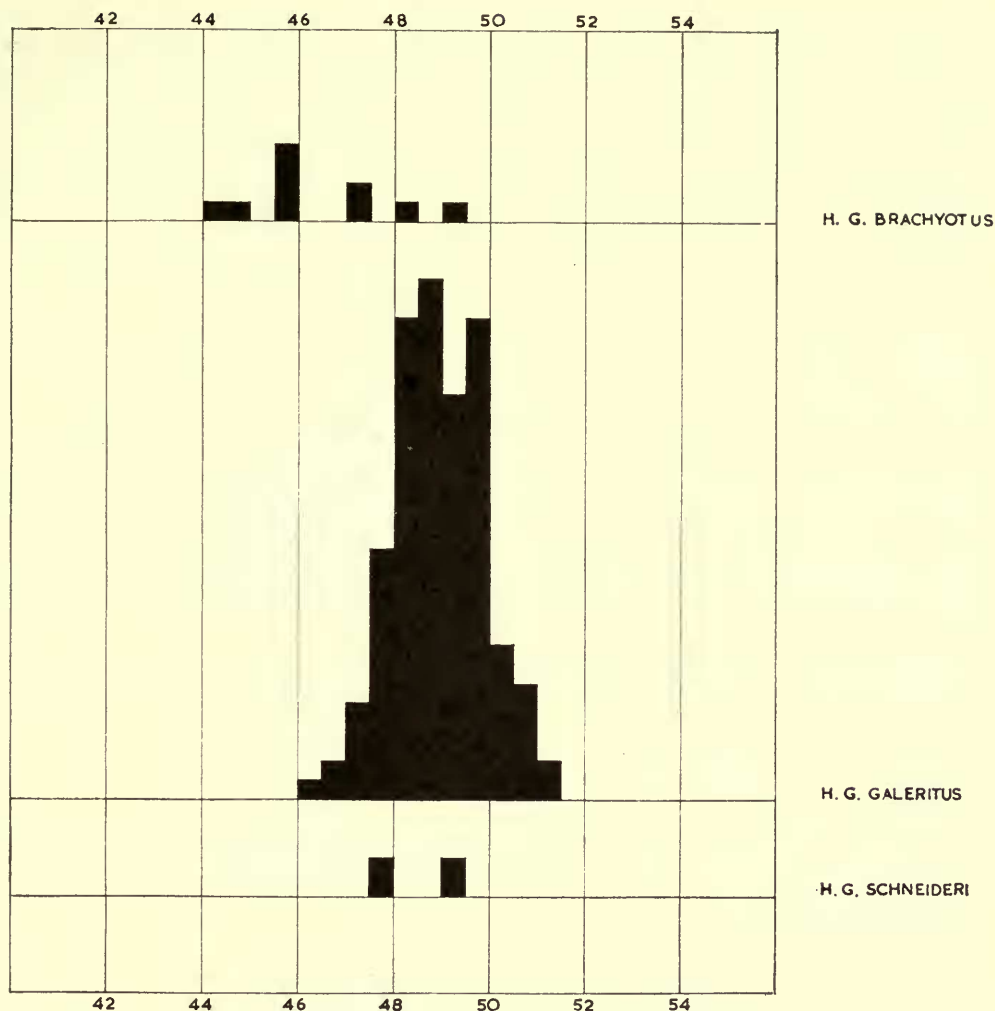
DISTRIBUTION : Sumatra ; Engano Island ; Sipora Island ; Mentawi Islands : North Pagi.

***Hipposideros galeritus labuanensis* (Tomes)**

Phyllorhina labuanensis Tomes, 1859a : 537. Labuan Island.

Hipposideros insolens Lyon, 1911 : 129. Upper Pasir River, southeastern Borneo.

This subspecies is very similar to *H. g. galeritus*. The post-palatal spicule may be present or absent and there is a well-defined sphenoidal depression. The upper incisors are not bilobed or only slightly so, and the upper canines have well defined anterior and posterior cusps. The anterior upper premolar (pm^2) is small, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third to one half the length of the anterior ridge. The anterior lower premolar (pm_2) is reduced to

FIG. 12. Length of forearm in *Hipposideros galeritus*

one half or a little less the length and height of the second lower premolar (pm_4) to two thirds its length and height. Davis (1962 : 39) provides a description, with measurements, of a series of *H. g. labuanensis* from North Borneo.

Lyon originally described *H. insolens* as a species distinct from *H. galeritus*, recording both from the same localities in Borneo. According to Lyon the distinguishing characters of *H. insolens* were its longer forearm and tibia when compared with *H. galeritus*. Chasen (1940 : 46) listed *H. insolens* as a subspecies of *H. longicauda*, here considered to be a subspecies of *H. galeritus*. Tate (1941 : 368) retained *H. insolens* as an apparently distinct species and from an examination of the original series described by Lyon stated that in comparison with *H. g. labuanensis*

the jugal prominence of the zygoma in *H. insolens* rose more abruptly, the ante-orbital foramen was almost pore-like and not elongate as in *H. g. labuanensis* while the palate was a little longer (extending a little behind the second upper molar) and lacked a spine. He also noted that the tooththrow was shorter, with the W-pattern of the third upper molar less reduced and that the anterior lower premolar (pm_2) was more elongate than wide. No topotypical specimens of *H. insolens* are available but the collections of the British Museum (Natural History) contain an adequate series of *Hipposideros galeritus* from Borneo and this series suggests that *H. insolens* as understood by Lyon and Tate may well refer to large individuals of *H. g. labuanensis*. The jugal prominence in a long series of *H. g. labuanensis*, although usually moderate in its development is sometimes found to be not greatly developed, rising only gently from the zygoma while the anteorbital foramen, usually elongate, is on occasion rounded and more pore-like. The rear of the palate varies from a line joining the posterior faces of the second upper molars (m^{2-2}) to a line joining the centres of the third upper molars (m^{3-3}), while the post-palatal spicule is sometimes absent or incipient. The length of the posterior ridge of the third upper molar varies from one third to one half the length of the anterior ridge, while the anterior lower premolar (pm_2) varies from less than one half the length and height of the second lower premolar (pm_4) to two thirds its length and height.

DISTRIBUTION : Borneo ; Labuan Island ; Philippine Islands : Mindanao (Sanborn (1952 : 104) as *H. g. galeritus* : see also Laurie & Hill (1954 : 55)).

Hipposideros galeritus longicauda (Peters)

Phyllorhina longicauda Peters, 1861 : 708. Java.

There are no specimens of this subspecies in the collections of the British Museum (Natural History). Sody (1930 : 270) describes four specimens in some detail.

DISTRIBUTION : Java.

Hipposideros galeritus celebensis Sody

Hipposideros celebensis Sody, 1936 : 47. Mampoe Cave, 20 kilometres north of Watoe Pone, south Celebes.

There are no specimens of this subspecies in the collections of the British Museum (Natural History). A detailed description (as *H. g. galeritus*) is given by Sody (1930 : 268) of specimens from Celebes subsequently described by the same author as *H. celebensis*.

DISTRIBUTION : Celebes.

Hipposideros galeritus batchianus Matschie

Hipposideros batchianus Matschie, 1901 : 273. Batchian Island, Molucca Islands.

There is no example of this subspecies in the collections of the British Museum (Natural History).

Hipposideros galeritus cervinus (Gould)

Rhinolophus cervinus Gould, 1863 : pl. 34, letterpress. "Caves on Albany Island" (label on skin of type specimen). Cape York, northern Queensland, Australia.

The characters of this subspecies are largely those of the nominate subspecies, the anterior upper premolar (pm^2) reduced, extruded from the tooththrow, the canine

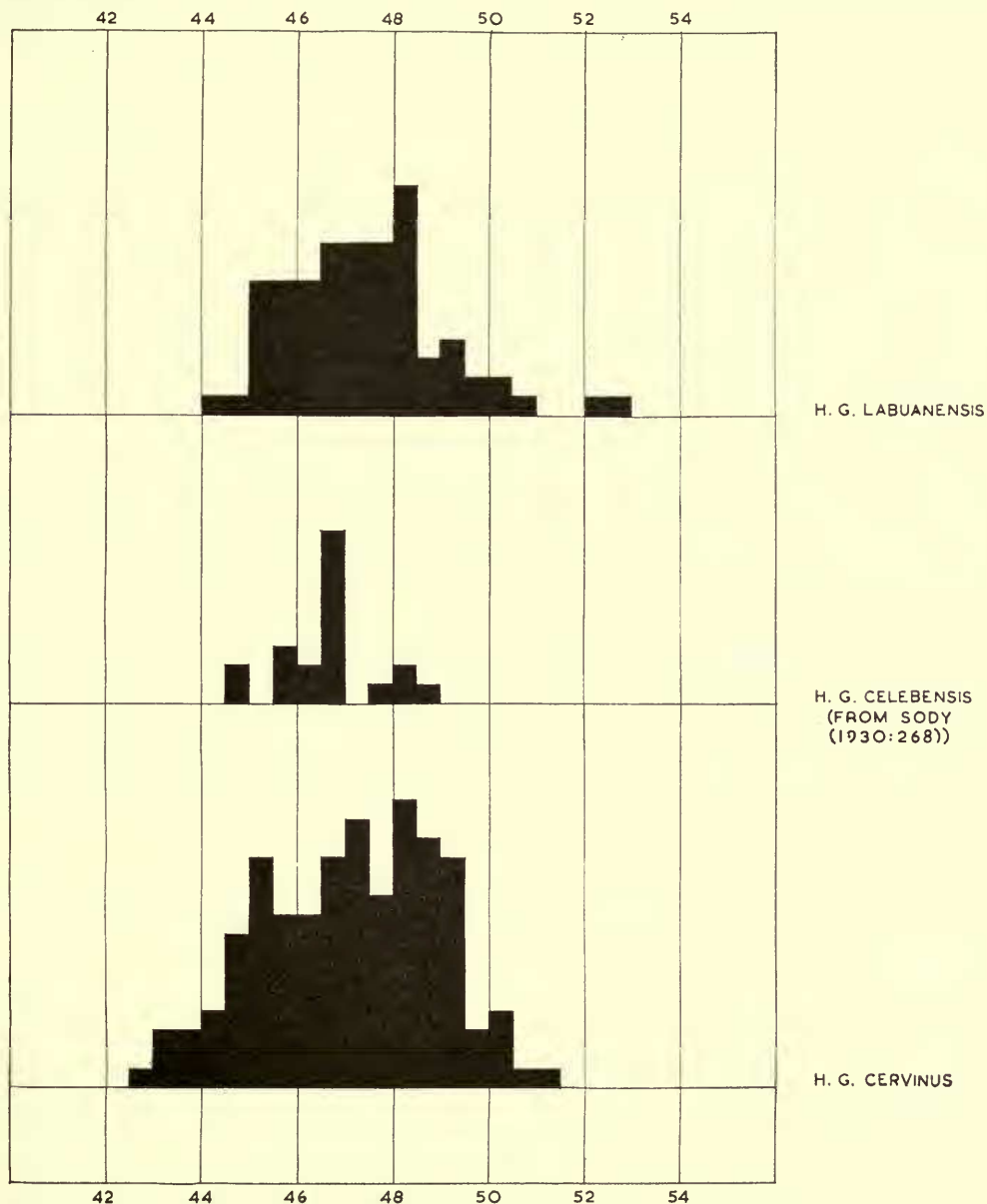


FIG. 13. Length of forearm in *Hipposideros galeritus*

and the second upper premolar (pm^4) in contact or nearly so and the anterior lower premolar (pm_2) usually one half or less the length and height of the second lower premolar (pm_4). Specimens from the Aru Islands have the anterior upper premolar (pm^2) much reduced, sometimes minute while in those from the Kei Islands this tooth is minute, almost invisible. Specimens from both groups of islands have the anterior lower premolar (pm_2) usually less than one half the length and height of the second lower premolar (pm_4). Those from Japen Island have a small but clearly visible anterior upper premolar (pm^2) and have the anterior lower premolar (pm_2) one half the length and height of the second lower premolar (pm_4). In specimens from New Guinea the anterior upper premolar (pm^2) is rather larger and more prominent while the anterior lower premolar (pm_2) is one half the length and height or slightly more of the second lower premolar (pm_4). Examples from New Ireland, the Solomon Islands, the New Hebrides and Cape York exactly resemble those from New Guinea but a single specimen from Kiriwina Island has the anterior lower premolar (pm_2) larger, equal nearly to two thirds the length and height of the second lower premolar (pm_4). There is some size variation over the range, specimens from the Aru and Kei Islands, Japen Island, Cape York and the Solomon Islands having the forearm averaging slightly shorter than those from New Guinea and the New Hebrides.

DISTRIBUTION : New Guinea ; Waigeo Island ; Japen (= Jobi) Island ; Kei Islands ; Aru Islands ; northern Australia ; Bismarck Archipelago : New Ireland ; Trobriand Islands : Kiriwina ; Solomon Islands : Bougainville ; Guadalcanar ; Fauro ; Russell ; Rennell ; New Hebrides : Espiritu Santu ; Efate ; Santa Cruz Islands : Fenvaloa ; Vanikoro.

Hipposideros crumeniferus (Lesueur & Petit)

Rhinolophus crumeniferus Lesueur & Petit, 1807 : pl. 35. Timor Island.

The status of this early name has already been discussed. Despite a careful search by the authorities of the Muséum National d'Histoire Naturelle in Paris, no trace can be found of the type specimen.

Hipposideros breviceps Tate

Hipposideros breviceps Tate, 1941 : 358. North Pagi Island, Mentawai Islands, off west coast of Sumatra.

Through the courtesy of the authorities of the American Museum of Natural History, New York, I have been able to examine two of the paratypes of *H. breviceps* Tate. The ears are broad, triangular, their anterior margins convex and their posterior margins with a concavity behind the acute point but otherwise convex. No definite internal fold can be discerned in the dry skins, but the membrane of the ears is thickened at the antitragal lobe. The ears are haired for one half or slightly more of their length. The noseleaf is small, with two lateral supplementary leaflets projecting beyond the margins of the anterior leaf. The anterior lateral

supplementary leaflet extends from the base of the intermediate part of the leaf anteriorly beneath the anterior leaf on to the upper lip, but does not reach the median line. The posterior leaflet does not extend forward in the same manner but terminates anteriorly at a point just on the upper lip. The anterior leaf has no median emargination, and the internarial septum is undeveloped. The narial lappets are well developed and project above the level of the anterior leaf. The nostrils lie in deep depressions but are not pocketed, while the intermediate part of the leaf is slightly inflated and cushion-like. The posterior leaf is high, its upper edge semi-circular, and is supported by the median septum and two lateral septa.

The skull is very short and broad, with an inflated, broadened braincase and low sagittal crest. The interorbital region is moderately constricted and the supra-orbital ridges are poorly defined. There is a shallow frontal depression. The rostrum is rounded and not markedly pentagonal in outline, with the rostral eminences much inflated and individually swollen, separated by a groove. The zygomata are slender, with a high, well developed jugal projection, the zygomatic width exceeding the mastoid width. The anteorbital foramen is elongate, closed by a narrow bar. The premaxillae are short and do not project beyond the canines, making a shallowly V-shaped junction with the maxillae. The palate is short, the palation shallowly U-shaped, level with a line joining the posterior faces of the third upper molars (m^{3-3}), without a post-palatal spicule. The mesopterygoid fossa is wide, the vomer not projecting, and the expanded pterygoids are long, together with the wide sphenoidal bridge almost concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are a little wider than their distance apart. The upper incisors are weakly bilobed, the outer lobe obsolescent and are strongly convergent, their tips almost touching. The upper canines have a small posterior cusp. The anterior upper premolar (pm^2) is minute and completely extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors is very slightly greater than the crown area of the inner lower incisors, while the anterior lower premolar (pm_2) is very small, one quarter or little more the length and height of the second lower premolar (pm_4).

Externally, *H. breviceps* is very similar to *H. galeritus*, but has the ears slightly less extensively haired. The skull closely resembles that of *H. galeritus* but is relatively shorter, with more inflated rostral eminences. In the shortening of the skull it tends towards *H. dyacorum* and this feature, together with the reduction of the anterior premolars, no doubt led Tate (1941 : 358) to consider *H. breviceps* as a half-way stage between an *insolens*-like form and *dyacorum*. However, there appears to be no close relation between *H. breviceps* and *H. dyacorum*. The ears of *H. dyacorum* have a well-defined internal fold, absent in *H. breviceps*, while the noseleaves of the two species differ sharply in the absence of lateral supplementary leaflets in *H. dyacorum* and the presence of two well-developed leaflets in *H. breviceps*. The skull of *H. breviceps*, although similar in outline to that of *H. dyacorum*, is less shortened, and has a much less constricted interorbital region.

There is a shallow frontal depression, absent in *H. dyacorum*, and there are no marked supraorbital ridges like the prominent, sharply defined ridges of that species. *Hipposideros breviceps* has the palate less shortened than *H. dyacorum* and its palation lacks a median emargination: it has a wider mesopterygoid fossa and wider, more spreading pterygoids, with an unconstricted sphenoidal bridge. The affinities of *H. breviceps* clearly lie with *H. galeritus*, from which it differs in a number of cranial features, such as its relatively shorter skull and less well-defined supraorbital ridges, slightly more inflated rostral eminences, shorter premaxillae, shorter palate and strongly convergent upper incisors. It is approached most nearly by *H. g. schneideri*, which closely resembles *H. breviceps* and has a similarly shortened skull, but which is larger and has rather more prominent supraorbital ridges, less inflated rostral eminences and longer premaxillae. The dentition of *H. g. schneideri* is almost identical with that of *H. breviceps*, with the anterior upper premolar (pm^2) minute or absent and the anterior lower premolar (pm_2) much reduced. The upper incisors of *H. g. schneideri*, however, are much less strongly convergent at their tips than in *H. breviceps*, in which the tips almost touch, and the anterior lower premolar (pm_2) is slightly less reduced. The majority of its characters indubitably ally *H. breviceps* closely to *H. galeritus*, with which it is apparently sympatric in the Mentawai Islands (Tate (1941: 368, 391) records *H. g. schneideri* from North Pagi Island) and it is considered to be a recently derived species, close to *H. galeritus* and having much the same relationship to that species as *H. beatus* has to *H. caffer* in the Ethiopian region.

DISTRIBUTION : Mentawai Islands : North Pagi Island.

Hipposideros curtus G. M. Allen

Hipposideros curtus G. M. Allen, 1921 : 194. Sakbayème, Cameroons.

Hipposideros sandersoni Sanderson, 1937 : 290, 296. Near Mamfe, Nigeria.

The ears are very large and broad, rather rounded and bluntly pointed, with a sharp concavity behind the tip. There is a small antitragal fold and they are haired for one half their length. The noseleaf is broad, with two small lateral supplementary leaflets. The anterior leaf has a small median emargination. The internarial septum is swollen and inflated, especially posteriorly between the nostrils, where it forms a slightly disc-like structure, the disc not however concealing the nostrils. The intermediate part of the leaf is cushion-like, with a low median eminence. The posterior leaf is high, its upper edge semicircular, and is supported by three septa enclosing deep pockets. A frontal sac is present in both sexes.

The skull is small, short and broad, with a low sagittal crest. The interorbital region is moderately constricted, with ill-defined supraorbital ridges. The frontal region is more or less pentagonal as in *H. galeritus*, with a shallow frontal depression and well-inflated rostral eminences separated by a shallow groove. The zygomata are moderate with a low jugal projection and the anteorbital foramen is large and rounded, closed by a narrow bar. The premaxillae make a V-shaped junction with the maxillae and the palate is short, with a square palation. The mesopterygoid

fossa is wide with a slightly projecting vomer, while the pterygoids are short, with a narrow, sharply constricted sphenoidal bridge exposing slightly elongate lateral apertures. There is a very shallow sphenoidal depression and the width of the cochleae is equal to their distance apart or is very slightly greater. The upper incisors are weakly bilobed and the upper canines shallowly grooved anteriorly, with low anterior and posterior cusps. The anterior upper premolar (pm^2) is small, slightly extruded but compressed between the canine and the second upper premolar (pm^4). The posterior ridge of the third upper molar is much reduced and obsolescent. The crown area of the outer lower incisors is a little greater than that of the inner lower incisors, while the anterior lower premolar (pm_2) is considerably reduced, to one half the length and one third the height of the second lower premolar (pm_4).

Hipposideros curtus, like *H. fuliginosus*, is a species evidently derived from the *bicolor-caffer* line and presents features which ally it to both the *bicolor* and *galeritus* sections of the *bicolor* group. Its external characters, especially the form of the ears, demonstrate its affinity to the *bicolor* subgroup but its short, broad skull tends towards the *galeritus* subgroup while *H. curtus* has also the short pterygoids and narrow sphenoidal bridge characteristic of *H. caffer* and its immediate allies.

DISTRIBUTION : West Africa : Cameroons ; Nigeria.

Hipposideros fuliginosus (Temminck)

Phyllorhina fuliginosa Temminck, 1853 : 77. " La côte de Guinée ".

The ears are large and broad, sharply triangular and acutely pointed, with a slight trace of an internal fold. Their posterior margins are slightly concave behind the tip, and they are haired for one half of their length. The noseleaf is comparatively broad, with two lateral supplementary leaflets, the anterior leaflet extending anteriorly for a short distance below the anterior leaf. The anterior leaf is simple with the internarial septum uninflated and with well-developed narial lappets. The intermediate part of the leaf is inflated, with a low median eminence. The posterior leaf is high, its upper edge semicircular and unlobulated. It lacks supporting septa but has a very low transverse structure, its upper edge not serrated, developed from its posterior face. There is no trace of a frontal sac in two male specimens (see also Hayman (1946 : 772)).

The skull is elongate, with a low to moderate sagittal crest. The interorbital region is long and relatively unconstricted, with barely defined supraorbital ridges. There is no frontal depression and the rostral eminences are moderately inflated and separated by a shallow trough. The zygomata are slender with a moderate jugal projection and the anteorbital foramen is elongate and closed by a narrow bar. The anterior palatal foramina are elongate and not enclosed by the premaxillae, which make a V-shaped junction with the maxillae. The palation is square with a shallow median emargination. The mesopterygoid fossa is wide with long, moderately expanded pterygoids which partially conceal elongate lateral apertures. The sphenoidal bridge is moderately constricted and there is a moderate sphenoidal depression. The cochleae are rather less in width than their distance apart. The

upper incisors bear only a trace of the outer lobe and the upper canines have a shallow groove on their anterior faces, with weak anterior and posterior cusps. The anterior upper premolar (pm^2) is much reduced, extruded, with the canine and the second upper premolar (pm^4) almost in contact. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors slightly exceeds that of the inner lower incisors, and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4).

There is little doubt that *H. fuliginosus* is a derivative of the line leading from *H. bicolor* and its allies to the more specialized *H. caffer*, possessing certain features common to the *bicolor* subgroup and others common to the *galeritus* subgroup, to which *H. caffer* is allocated. It has broad, sharply triangular ears, two lateral supplementary leaflets and the posterior leaf, which lacks supporting septa, has a low transverse structure developed from its posterior face. These features ally it to *H. caffer*: however, its skull is elongate with the long interorbital region characteristic of the members of the *bicolor* subgroup.

DISTRIBUTION : West Africa : Liberia ; Togo ; Ghana ; Nigeria ; Cameroons ; Gaboon ; Congo.

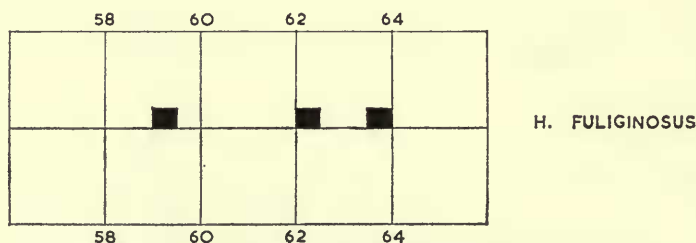


FIG. 14. Length of forearm in *Hipposideros fuliginosus*

Hipposideros caffer

The ears are large, broad, triangular and acutely pointed. Their posterior margins are concave just behind the tip. There is a slight thickening at the antitragal fold and the ears are haired for two thirds to three quarters of their length. The nose-leaf is comparatively simple with two lateral supplementary leaflets, the anterior leaflet extending anteriorly beneath the anterior leaf, sometimes reaching or almost reaching the median line. The anterior leaf is simple and has no median emargination. The internarial septum is slightly inflated. The intermediate part of the leaf is cushion-like, with a low to moderate median eminence, sometimes with low lateral eminences. The posterior leaf is thin, its upper edge semicircular, unlobulated and lacks supporting septa. Its posterior face bears a transverse supplementary structure with a serrated upper edge below that of the true posterior leaf. A frontal sac is present in both sexes but is very small in females.

The skull is short and broad, closely similar in outline to the skull of *H. galeritus*. The braincase is broad with a low sagittal crest and the interorbital region is not

greatly constricted, the supraorbital ridges low but sharply defined. There is no frontal depression and the rostral eminences are moderately inflated. The zygomata have a high jugal process, set far back, and the anteorbital foramen is elongate, closed by a narrow bar. The premaxillae make a U-shaped or shallowly V-shaped junction with the maxillae and the anterior palatal foramina are slightly elongate, not enclosed within the premaxillae but almost closed posteriorly by the delicate anterior enclosing processes. The palation is nearly square with a small median notch while the mesopterygoid fossa is wide, the vomer not projecting and the pterygoids short, with a narrow, sharply constricted sphenoidal bridge exposing wide lateral apertures. There is a shallow sphenoidal depression. The cochleae are moderate, their width equal to or a little greater than their distance apart. The upper incisors are weakly bilobed, their outer lobes obsolescent. The upper canines have their anterior faces flattened or with a shallow, ill-defined groove and have a moderate anterior cusp and a slightly higher posterior cusp. The anterior upper premolar (pm^2) is small or very small, slightly extruded, compressed between the canine and the second upper premolar (pm^4), which usually are not in contact, sometimes more fully extruded with these teeth in contact or nearly so. The posterior ridge of the third upper molar is not greatly reduced, equal to one half the length of the anterior ridge or more. The crown area of the outer lower incisors is very slightly greater than that of the inner pair. The anterior lower premolar (pm_2) is not excessively reduced, one half or more the length and height of the second lower premolar (pm_4).

Hipposideros caffer is the principal representative of the *galeritus* subgroup in the Ethiopian region, and like *H. galeritus*, is the dominant and most widely distributed species of the subgroup in its region. Despite its superficial resemblance to *H. galeritus*, it differs widely from this and its associated species in the structure of its posterior noseleaf and in the characters of the post-palatal region. These differences suggest remote origin in the *bicolor* group although there seems little doubt that *H. galeritus* and *H. caffer* have developed from a common if remote source. Both are similarly specialized in a number of features, notably in the extent of body fur on the ears and in the number of lateral supplementary leaflets: both have a characteristic short broad skull very different from the elongate narrow skull of the *bicolor* type yet both can be linked to the *bicolor* subgroup by a series of species exhibiting a variety of features on the one hand found in *bicolor* and *galeritus* and on the other in *bicolor* and *caffer*.

A number of subspecies have been proposed to divide *H. caffer*, mainly on the basis of size, and there is considerable dimensional overlap between them. No attempt has been made in the present work to establish the validity of the named forms of *H. caffer* but there seems little doubt from the very large series from most parts of its range now preserved in the collections of the British Museum (Natural History) that the variation in size of the species is largely clinal. Smaller subspecies (*H. c. caffer*, *H. c. tephurus*) are found in the Yemen, in the eastern part of Africa, in North Africa and on the west coast south to Sierra Leone and the Gold Coast. A larger subspecies (*H. c. ruber*) replaces *H. c. caffer* in the west of Kenya, Uganda

and Tanganyika, extending westwards through the Congo, to be itself replaced in west Africa by another large subspecies (*H. c. guineensis*) and in Angola and south-west Africa by yet another large subspecies (*H. c. angolensis*). The distributional limits of the subspecies are difficult of definition, and series from some localities cannot be allocated with certainty to subspecies.

DISTRIBUTION : Yemen ; the greater part of Africa excluding the Sahara desert and the extreme south.

Hipposideros caffer caffer (Sundevall)

Rhinolophus caffer Sundevall, 1846 : 118. Near Port Natal.

Phyllorhina gracilis Peters, 1852 : 36, pl. 7, figs. 1-4, pl. 13, figs. 14-15. Tette, Lower Zambezi, Mozambique.

Phyllorhina bicornis Heuglin, 1861 : 4, 7. Kérén, Eritrea.

DISTRIBUTION : Yemen ; Eritrea ; Somaliland ; Sudan ; Ethiopia ; Kenya (part) ; Tanganyika (part) ; Southern Rhodesia ; Northern Rhodesia (part) ; Nyasaland ; Natal ; Transvaal ; Zanzibar ; Pemba Island ; Congo (part).

Hipposideros caffer tephurus Cabrera

Hipposideros tephurus Cabrera, 1906 : 358. Mogador, Morocco.

Hipposideros braima Monard, 1939 : 73, fig. 5. Bagingara, Portuguese Guinea (see Aellen (1956b : 26)). *Hipposideros braima* is further described and illustrated by Veiga-Ferreira (1949 : 193).

DISTRIBUTION : North Africa : Morocco ; Senegal (part) ; Nigeria (part) ; Sierra Leone (part) ; Ghana (part) ; Senegambia.

Hipposideros caffer ruber (Noack)

Phyllorhina rubra Noack, 1893 : 586, pl. 18, figs. 14-15. "Lugerrunjere Fluss", Tanganyika.

Hipposideros caffer centralis Andersen, 1906b : 275, 277. Entebbe, Uganda.

DISTRIBUTION : Tanganyika (part) ; Kenya (part) ; Uganda ; Congo (part) ; North Rhodesia (part) ; Angola (part) (Sanborn (1950 : 58)) ; recorded from Guinea by Aellen (1956a : 889).

Hipposideros caffer angolensis (Seabra)

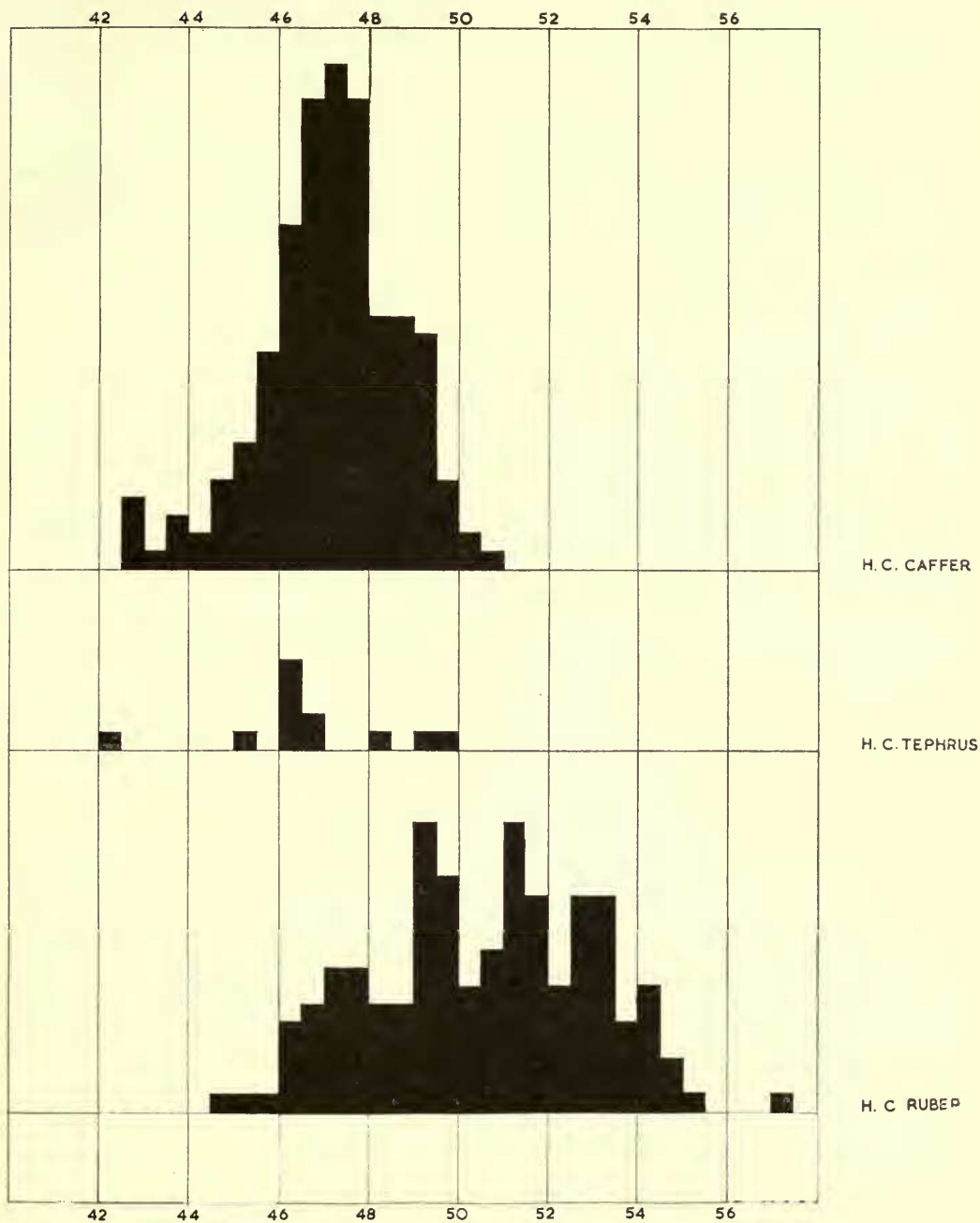
Phyllorhina angolensis Seabra, 1898 : 256. Rio Coroca, Angola.

DISTRIBUTION : Angola ; southwest Africa ; Gaboon (part) ; recorded from Ghana by Booth (1956 : 137).

Hipposideros caffer guineensis Andersen

Hipposideros caffer guineensis Andersen, 1906b : 275, 278. Como River, 70 miles from Gaboon.

DISTRIBUTION : Gaboon (part) ; Cameroons ; Nigeria (part) ; Ghana (part) ; Gambia ; Sierra Leone (part) ; Liberia ; San Thomé Island ; Principe Island ; Fernando Po ; Spanish Guinea ; Senegal (part) (Aellen (1956b : 26)).

FIG. 15. Length of forearm in *Hipposideros caffer*

***Hipposideros caffer niapu* J. A. Allen**

Hipposideros caffer niapu J. A. Allen, 1917 : 431. Niapu, northeastern Congo.

DISTRIBUTION : Congo (part).

Hipposideros beatus

The ears are large, broad, triangular and pointed. Their posterior margins are concave just behind the tip. There is a slight thickening at the antitragal fold and they are haired for two thirds of their length. The noseleaf exactly resembles

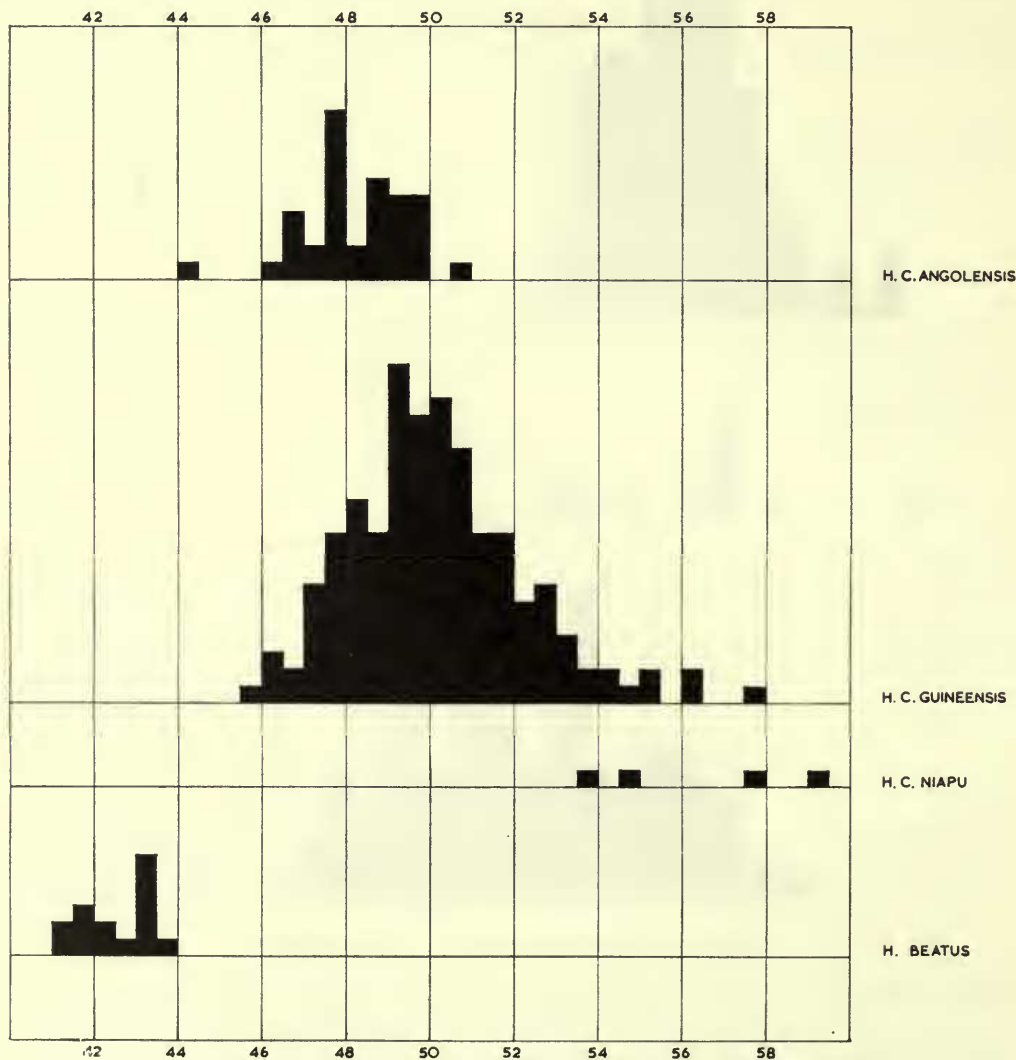


FIG. 16. Length of forearm in *Hipposideros caffer* and *H. beatus*

that of *H. caffer*. The skull is short and broad and very similar to that of *H. caffer*. There is a low sagittal crest and the interorbital region is only slightly constricted, with low but sharply defined supraorbital ridges. There is a very shallow frontal depression and the rostral eminences are inflated and separated by a shallow groove. The zygomata are slender, with a high jugal process, and the anteorbital foramen is rounded, closed by a narrow bar. The premaxillae make a V-shaped junction with the maxillae and the palation is square with a median notch. The mesopterygoid fossa is a little narrower than in *H. caffer*, the pterygoids short with a narrow, sharply constricted sphenoidal bridge exposing wide lateral apertures. There is a shallow sphenoidal depression and the width of the cochleae is equal to their width apart or is slightly greater. The upper incisors are weakly bilobed and the upper canines have a weak anterior cusp and a low but well developed posterior cusp. The anterior upper premolar (pm²) is minute, extruded, with the canine and the second upper premolar (pm⁴) in contact or nearly so. The posterior ridge of the third upper molar is one third or less the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than the crown area of the inner pair. The anterior lower premolar (pm₂) is a little more than one half the length and height of the second lower premolar (pm₄).

Hipposideros beatus differs only very slightly from *H. caffer*, and may be distinguished from that species chiefly by its smaller size and the greater degree of reduction of its anterior lower premolar (pm₂). The two species provide an interesting parallel in the Ethiopian region to the Asiatic species *H. galeritus* and *H. breviceps*, the latter differing only very slightly from the former. *Hipposideros beatus* is slightly more advanced than *H. caffer* in the details of its dentition and is regarded as a very close derivative of *H. caffer*.

DISTRIBUTION : West Africa from the Congo to Sierra Leone.

Hipposideros beatus beatus Andersen

Hipposideros beatus Andersen, 1906b : 279. 15 miles from Benito River, West Africa.

Hipposideros nanus J. A. Allen, 1917 : 434. Faradje, Uele District, eastern Congo.

Hayman (1936 : 919) thought that *H. nanus* Allen probably referred to the dark phase of *H. beatus*. Verschuren (1957 : 371) considered it to be a distinct species, distinguished chiefly by its colour and by the insertion of the wing membrane on the tibia and not on the metatarsals as in *H. beatus*. These features are variable in a small series of *H. beatus* and for the present *H. nanus* is provisionally retained in the synonymy of this species.

DISTRIBUTION : Congo (part) ; Cameroons ; Nigeria ; Ghana ; Liberia ; Sierra Leone.

Hipposideros beatus maximus Verschuren

Hipposideros beatus maximus Verschuren, 1957 : 362, 365. Pidigala-Nord, Parc National de la Garamba, Congo.

***Hipposideros coxi* Shelford**

(Figure 17)

Hipposideros coxi Shelford, 1901 : 113. Mount Penrisen, Sarawak, Borneo, 4,200 feet.

A species of medium size with very large, sub-triangular ears, broad at the base, bluntly pointed, with their anterior margins slightly concave in the upper portion, their posterior margins strongly so for the upper third, thereafter convex. The antitragal lobe is well developed, with a prominent internal fold, and the ears are haired for two thirds of their length. The noseleaf is large and forms a structure of extraordinary complexity, covering the entire muzzle, with two lateral supplementary leaflets. The anterior leaflet on each side extends anteriorly beneath the anterior leaf to become continuous over the upper lip, with no median emargination. At its upper or posterior end this leaflet terminates on each side in a small wart-like protuberance or papilla, at about the level of the eye, pierced by a minute pore. A small, sharply triangular pointed leaflet extends upwards from this papilla behind the lateral margin of the anterior leaf. This extension of the anterior supplementary leaflet at its upper end joins a further cutaneous leaflet extending from the rear of the intermediate part of the leaf, to which it is attached, downwards to a point just above the eye, forming a structure of the shape of an inverted Y. The lateral margin of the posterior leaf is joined to the upper surface of this cutaneous leaflet : the junction of the triangular extension of the supplementary leaflet is on its lower surface at a point nearer to the eye, these leaflets enclosing deep pockets behind the intermediate part of the leaf. Cutaneous outgrowths composed either of the anterior lateral supplementary leaflet or of extensions therefrom thus extend completely beneath the anterior leaf and beneath much of the margins of the intermediate part of the leaf, forming deep pockets beneath the latter. The posterior lateral supplementary leaflet is broad and extends from a point level with the wart terminating the anterior leaflet only for a short distance on to the muzzle, just reaching the upper lip. This observation is contrary to that of Shelford, who stated in the original description that the lower (or posterior) leaflet consisted of two separate parts : it is clear from the type specimen, however, that Shelford mistook the cutaneous leaflet extending downwards from the base of the posterior leaf to be a part of the posterior leaflet, but it is apparently a structure quite distinct from either of the lateral supplementary leaflets. The anterior leaf is very large, lacking a median emargination, completely covering the muzzle and with its margin projecting beyond the upper lip and concealing the anterior lateral supplementary leaflets, which however project beyond the lateral margins of the anterior leaf. The internarial septum is slightly bulbous anteriorly, dividing two deep pockets anterior to the nostrils. The narial region is greatly specialized, the narial lappets greatly developed and with their bases expanded towards the median line to join the internarial septum, forming deep pouches at the base of which the nostrils are situated. These pouches have slightly crescentic, elongate openings and the narial lappets project above the level of the anterior leaf. The intermediate part of the leaf is inflated with a prominent median ridge, sparsely haired at its upper end :

laterally, there are two low eminences on each side of this ridge, just beneath the upper margin of the intermediate part of the leaf. The lateral margins of the intermediate part of the leaf are extended laterally to form a triangular lappet on each side extending over the bases of the margins of the anterior leaf and over the bases of the lateral supporting septa of the posterior leaf. The posterior leaf is very high, thick, its upper edge rounded and is supported by three septa. The central or median septum is narrow and blade-like, with a large, deep cell flanking it on each side. The lateral septa are very broad, their upper ends continuous with the face of the posterior leaf, the cells external to these septa narrow but very deep. The upper third of the posterior leaf extends above these septa and in the type specimen (in alcohol) is folded back upon itself. Laterally, the margins of the posterior leaf extend downwards and are joined to cutaneous leaflets attached on each side to the rear of the lateral lappets of the intermediate part of the leaf. At their upper ends these leaflets form the floor of the deep lateral cells of the posterior leaf and the roof of deep pockets beneath the intermediate part of the leaf.

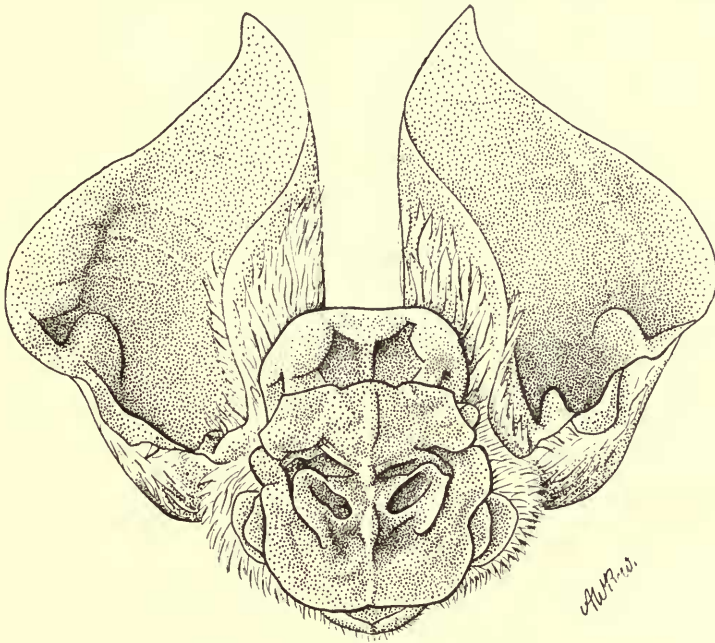


FIG. 17. *Hipposideros coxi* ♀ (Type B.M. 1.6.23.1) (x3)

The skull is elongate and comparatively narrow, with an elongate braincase and low sagittal crest. The interorbital region is not sharply constricted and there are no supraorbital ridges. There is no frontal depression and the rostrum is elongate and high, with the rostral eminences much inflated, separated by a shallow depression. The zygomata are slender with a low jugal projection and the zygomatic width is less than the mastoid width. The anteorbital foramen is small and rounded, separated from the orbit by a massive bar of bone enclosing a long anteorbital canal.

The premaxillae of the type specimen are missing. The palate is not markedly shortened, the palation shallowly V-shaped with a small post-palatal spicule. The mesopterygoid fossa is wide, the vomer not projecting, with long, expanded pterygoids and wide sphenoidal bridge almost concealing narrow, elongate lateral apertures. There is a shallow sphenoidal depression and the width of the cochleae slightly exceeds their distance apart. The upper canines have low anterior and posterior cusps and the anterior upper premolar (pm^2) is very small, extruded from the toothrow, with the canine and the second upper premolar (pm^4) almost in contact. The second anterior upper premolar (pm^4) has a well-developed anterior cusp. The posterior ridge of the third upper molar is one half the length of the anterior ridge. The crown area of the outer lower incisors slightly exceeds that of the inner pair and the anterior lower premolar (pm_2) is slightly over one half the length of the second lower premolar (pm_4) and is one half of its height.

Hipposideros coxi is very sharply removed from the other species of the *bicolor* group by the great specialization of its noseleaf, which in the degree of its complexity is approached by no other species of the group. Certain features, however, ally it to the *bicolor* group. Its ears are of the *bicolor* type, with a well-developed internal fold. The anterior lateral supplementary leaflet extends beneath the anterior leaf to reach the median line: a similar condition is found in *H. jonesi* and *H. pygmaeus*, which have the leaflets divided above the centre of the upper lip by a deep emargination. There is no such emargination in *H. coxi*, and the anterior lateral supplementary leaflets form an uninterrupted cutaneous frill beneath the anterior leaf. Narial pockets surrounding the nostrils, greatly developed in *H. coxi*, are less pronounced in *H. pygmaeus* and are developed to some extent in *H. obscurus*. The elongate skull and narrow zygomata of *H. coxi* demonstrate its affinity to the *bicolor* subgroup, but its complex noseleaf and long anteorbital canal, enclosed by a massive bar of bone, clearly remove it from any close relation to the members of this subgroup or of the *galeritus* subgroup. Its great degree of specialization suggests that *H. coxi* must be considered an isolated species of remote origin and it is probably derived from the basal stem of the *galeritus* subgroup.

Hipposideros papua (Thomas & Doria)
(Figure 18)

Phyllorhina papua Thomas & Doria, 1886: 204. Korido, Misor Island, Geelvinck Bay, Netherlands New Guinea.

(?) *Phyllorhina cervina* var. *misorensis* Peters, 1906: pl. 5L, figs. 4, 4a, 4b.

The ears are long, broad and triangular, acutely pointed, their posterior margins forming a smooth convex curve. There is a small, slightly thickened antitragal fold and the ears are apparently haired for one third or a little more, perhaps one half of their length (the syntype and only available specimen has the skin in bad condition). The noseleaf is broad, covering the entire muzzle, with three lateral supplementary leaflets, the first normal, extending upwards to the base of the posterior leaf just anterior to the eye, the central or second leaflet extending from a point below and just anterior to the eye anteriorly beneath the anterior leaf on to the

upper lip but not reaching the median line and the third leaflet very small, rudimentary and incipient. The anterior leaf is large, extending over the upper lip, but has no median emargination. The internarial septum is uninflated and the narial lappets well developed, with the internarial septum forming shallow narial pockets. The intermediate part of the leaf is simple with a low median ridge. The posterior leaf is high, its upper edge semicircular and thickened and is supported by three moderate septa enclosing shallow pockets. There is a small depression but no frontal sac in the female type specimen.

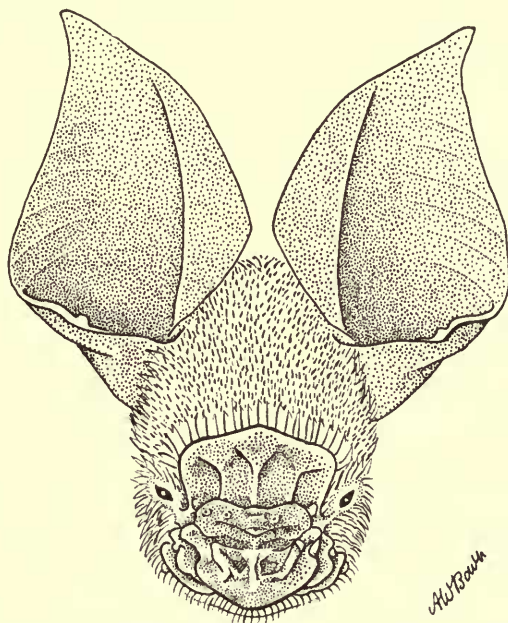


FIG. 18. *Hipposideros papua* ♀ (Syntype B.M. 86.11.3.9) (x3)

The skull is only slightly elongate, with a long, broadened braincase and moderate sagittal crest. The interorbital region is moderately constricted with barely defined supraorbital ridges. There is a moderate frontal depression, and the rostrum is slightly broadened, with well-inflated rostral eminences separated by a shallow groove. The zygomata are slender, with a moderate jugal process, and the ante-orbital foramen is large, elongate and closed by a narrow bar. The premaxillae make an acutely V-shaped junction with the maxillae and the anterior palatal foramina are elongate and not totally enclosed. The palate is not markedly shortened, the palation U-shaped with a small post-palatal spicule. The mesopterygoid fossa is moderate and not greatly widened, the vomer not projecting and the pterygoids long with a wide sphenoidal bridge, almost completely concealing elongate lateral apertures. There is a moderate sphenoidal depression and the width of the cochleae is slightly greater than their distance apart. The upper incisors are not bilobed and the upper canines have low anterior and posterior cusps. The anterior upper premolar (pm^2) is small and is only slightly out of alignment in the tooththrow.

The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is equal to that of the inner pair and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4).

Tate (1941 : 369, 387) was uncertain of the taxonomic position of *H. papua* and regarded it as a perplexing species. Its ears and cranial characters suggest affinity with the *bicolor* group, but *H. papua* has a specialized noseleaf which indicates no close connection with any of the members of that group. Some affinity to the *cyclops* group is suggested by the extension of the second lateral leaflet beneath the anterior leaf, a feature otherwise peculiar to *cyclops* and its allies, but *H. papua* differs from these in its broad ears, the presence of an incipient third leaflet, unenlarged bullae and convergent toothrows. A more tenuous affinity to the *speoris* group may be indicated by the presence of a rudimentary third leaflet. For the present *H. papua* must be regarded as a species of remote origin within the *bicolor* group, associated probably with the line leading to the *muscinus* group and less certainly with that leading to the *speoris* group.

HIPPOSIDEROS CYCLOPS group

The *cyclops* group as here understood includes the *cyclops* and *muscinus* groups of Tate (1941), both characterized by the great development of the ears and auditory region. The group includes six species, *H. cyclops*, *H. camerunensis*, *H. muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis*, all demonstrating a high degree of modification and specialization. The ears are long, narrow and acutely pointed, lacking any antitragal modification and not extensively haired. The noseleaves are much specialized, with two lateral supplementary leaflets. The anterior lateral supplementary leaflet is small, the posterior leaflet larger, extending posteriorly to the base of the posterior leaf, of which it forms a continuous part and in the majority of species extending anteriorly beneath the anterior leaf. The anterior leaf has no median emargination and the internarial septum is uninflated or only slightly thickened. The intermediate part of the leaf is flat or slightly cushion-like, specialized by the development to a greater or lesser degree of a median tubercle. The posterior leaf is moderate, with three supporting septa, its upper edge more or less semicircular, thickened, usually with a median club-like process (*H. cyclops*, *H. camerunensis*, *H. muscinus*, *H. semoni*, *H. stenotis*) or with a transverse supplementary structure developed from the posterior face of the leaf (*H. wollastoni*). The frontal sac is usually absent.

The skull is short and broad, the braincase wide and almost globose, with a low sagittal crest. The interorbital region is much constricted, with low supraorbital ridges. The rostrum is greatly broadened, with well-inflated rostral eminences. The zygomata are slender or moderate, with a low jugal process, and the anteorbital foramen is rounded, closed by a narrow bar, or pore-like. The palate is short and the pterygoids are long, together with the wide sphenoidal bridge almost concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are greatly developed, their width equal to four or more times their distance apart. The outer lobe of the upper incisors is obsolescent or absent and the upper canines

in most cases lack cusps but have well-developed cingula. The anterior upper premolar (pm^2) is usually much reduced and is absent in one species. The posterior ridge of the third upper molar is obsolescent or well developed, in some species almost complete with the W-pattern of the tooth virtually complete. The anterior lower premolar (pm_2) is much reduced.

The group is one of restricted distribution, with two species in the Ethiopian region and the remainder in New Guinea and northern Australia. As might be expected from this markedly discontinuous range, the group can be divided readily into two sharply defined sections, corresponding to the *cyclops* and *muscinus* groups of Tate (1941). Despite this sharp division, the two sections share features in common that make their independent origin unlikely. Their specialized ears and auditory region are unknown elsewhere in *Hipposideros*, as is the rearward extension of the posterior lateral supplementary leaflet to form a continuous part of the posterior leaf. The noseleaves are further specialized by the development of club-like projections, of which Tate (1941 : 379) observes that they are "structures so peculiar, specialized and seemingly functionless that they are unlikely to have arisen independently". The two sections share further the same typically shortened, broadened pattern of skull, unwidened at the mastoid region and with wide pterygoids and greatly enlarged cochleae.

The Ethiopian species *H. cyclops* and *H. camerunensis* are clearly the most primitive members of the group and may be readily distinguished from the Australasian species *H. muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis* by their much larger size. Their noseleaves differ markedly from those of the Australasian species in that the posterior lateral supplementary leaflet does not extend anteriorly beneath the anterior leaf, while the skulls of the Ethiopian species are more elongate than those of *H. muscinus* and its allies. The interorbital region is less sharply constricted in the Ethiopian species, and the rostral swellings, although inflated, are less swollen and more ossified. The premaxillae are wide and completely enclose narrow, elongate anterior palatal foramina, making a broad junction with the maxillae extending over almost the entire width of the palatal emargination in contrast to the narrow premaxillae of the Australasian species, which do not enclose the large oval anterior palatal foramina and which make a narrow junction with the maxillae, extending over only one third of the width of the palatal emargination. The cochleae are large but are less developed than those of the Australasian species, and are equal in width to approximately four times their distance apart.

Hipposideros muscinus and its allies, confined to New Guinea and northern Australia, are much smaller and more specialized than *H. cyclops* and its close relative *H. camerunensis*. The noseleaves of the Australasian species are characterized by a number of specializations, among which the forward extension of the posterior lateral supplementary leaflet beneath the anterior leaf is the most noticeable. These species have the skull much shortened, especially in the rostral region, with a broad braincase and a constricted interorbital region. As in *H. cyclops* and *H. camerunensis*, the inflated braincase is not abruptly widened at the level of

the mastoids. The interorbital region is short and much less elongate than in *H. cyclops* and *H. camerunensis*, while the rostrum, although broadened, is rounded and less angular. As in *H. cyclops* and *H. camerunensis*, the Australasian species have long pterygoids and a wide sphenoidal bridge, but the cochleae are more greatly expanded, their width in the majority of species equal to six or more times their distance apart. These differences suggest comparatively remote separation of the parental stocks of the two sections: *H. cyclops* and *H. camerunensis* have retained to some extent the elongate outline of the skull typical of the *bicolor* group, particularly in the elongate, broadened braincase, although the rostrum and palate are shortened, while *H. muscinus* and its allies are rather more specialized and represent a further trend of modification within the group.

Although *H. muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis* are closely related, it is possible to discern a weak division among them. *Hipposideros muscinus* is the least specialized: the tubercles on its intermediate and posterior noseleaves are not greatly developed, it lacks a frontal depression, its anteorbital foramen is elongate, closed by a narrow bar, there is a shallow sphenoidal depression traversed by a low median ridge and its cochleae are the least expanded, in width equal to approximately four to five times their distance apart. The anterior upper premolar (pm^2) is not greatly extruded and the posterior ridge of the third upper molar is small, less than one third the length of the anterior ridge, with the W-pattern of the tooth incomplete. *Hipposideros wollastoni*, despite the divergence of its posterior noseleaf, is cranially very similar to *H. muscinus*. However, its rostral eminences are rather more swollen, its anteorbital foramen is rounded, closed by a narrow bar, the sphenoidal bridge is less constricted, the sphenoidal depression not traversed by a median ridge and the cochleae more expanded, their width equal to six times their distance apart. The anterior upper premolar (pm^2) is small, extruded and the posterior ridge of the third upper molar is less reduced, one third or a little more the length of the anterior ridge, with the W-pattern of the tooth less incomplete.

Hipposideros semoni and *H. stenotis* are more closely related to each other than to *H. muscinus* or *H. wollastoni*, although their affinities as demonstrated by the noseleaves clearly lie nearer to *H. muscinus* than to *H. wollastoni*. In both *H. semoni* and *H. stenotis* the tubercles on the intermediate and posterior noseleaves are developed into club-like processes similar to those of *H. cyclops*. Cranially, both have a frontal depression and the anteorbital foramen is small and rounded, closed in *H. semoni* by a moderate bar and in *H. stenotis* by a narrow bar. In both the sphenoidal bridge is slightly more constricted than in *H. muscinus* or *H. wollastoni*. Neither *H. semoni* nor *H. stenotis* has a sphenoidal depression and in both the cochleae are greatly expanded, their width equal to eight times their distance apart. In *H. semoni* the anterior upper premolar (pm^2) is small and extruded from the tooth-row: it is absent in *H. stenotis* while in both the posterior ridge of the third upper molar is not greatly reduced and is equal nearly in length to the anterior ridge, the W-pattern of the tooth nearly complete. In view of these considerations I am unable to agree with Tate (1941: 379) that there can be no doubt that *H. muscinus*, *H. semoni* and *H. stenotis* are conspecific: although the available material

is limited, it is evident that *H. muscinus* is widely separated from *H. semoni* and *H. stenotis*, although these by comparison are closely related, as Tate (p. 389) recognized.

Tate (1941 : 378, 379) has provided an account of the *muscinus* group as he understood it, evidently based on series from various localities in Papua which he considered to represent *H. muscinus* (pp. 379, 386, 392). Furthermore, he notes (p. 386) that "there is no doubt that *muscinus* is very closely related to *semoni* and *stenotis*" and after reviewing some of the features of the ears and noseleaf of *H. muscinus* as given by Thomas & Doria in the original description states that the skull, which they did not describe, as represented by the syntype in the British Museum (Natural History) "shows the characteristics of *semoni* and agrees with my topotypical series of *muscinus* : the parallel toothrows, the greatly enlarged rostrum, the closely approximated cochleae, etc.". A comparison of his detailed account (pp. 378, 379) with the syntype of *H. muscinus* in the British Museum (Natural History) suggested that the specimens that Tate used as the basis of his study and that he referred to *H. muscinus* in fact did not represent that species but should be referred to *H. semoni*. Through the courtesy of the authorities of the American Museum of Natural History I have been able to examine a part of this series of specimens, including three of those from the Fly River, Papua, thought topotypical of *H. muscinus* by Tate. Comparison of this selection of the specimens studied by Tate with the syntype of *H. muscinus* and with examples of *H. semoni* in the collections of the British Museum (Natural History) shows that without doubt they represent the latter species.

A specimen preserved in alcohol, A.M.N.H. 108684, a male from the bank of the Fly River, opposite Sturt Island, Papua, has the noseleaf as described by Tate, its intermediate and posterior leaves with club-shaped median protuberances. These can be readily discerned in four other dry skins from Papua, A.M.N.H. 105341, a female from the same locality ; A.M.N.H. 105057, a male from five miles below Palmer Junction, Upper Fly River ; A.M.N.H. 108500, a young female from Baruari, Astrolabe Range, Central Division and A.M.N.H. 108504, a male from Sogeri, Central Division. These protuberances in the syntype of *H. muscinus* are not developed into club-shaped structures as in *H. semoni* and *H. stenotis* but take the form of tubercles. The skulls of the four dry specimens are available for study and agree exactly with the account by Tate. All have a small frontal depression, absent in *H. muscinus* but present in *H. semoni*. The anteorbital foramen is small, rounded and separated from the orbit by a moderate bar as in *H. semoni* : in *H. muscinus* this aperture is not rounded but is elongate and is separated from the orbit by a narrow bar. There is a low median sphenoidal ridge and no sphenoidal depression as in *H. semoni* : a shallow sphenoidal depression is present in *H. muscinus*. The cochleae are very large, their width equal to six or eight times their distance apart as in *H. semoni* : those of *H. muscinus* are less expanded with their width equal to four or five times their distance apart. The angular process of the mandible is elongate, connected to the articular process by a thin web of bone. This condition is very evident in *H. semoni*, which in this respect exactly resembles the series

studied by Tate as represented by these specimens : it is much less pronounced in *H. muscinus*. The anterior upper premolar (pm^2) is minute, extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact : this is the condition exhibited by *H. semoni* and not by *H. muscinus* in which the anterior upper premolar is larger and separates the canine and the second upper premolar. The posterior ridge of the third upper molar is nearly as long as the anterior ridge, the W-pattern of the tooth almost complete, as in *H. semoni* and *H. stenotis* : in *H. muscinus* the posterior ridge is less than one third the length of the anterior ridge and the W-pattern of the tooth is incomplete.

These specimens must be referred to *H. semoni* and agree exactly with A.M.N.H. 154710, a female from Upper Nesbit River, Cape York, Queensland (labelled *Hipposideros muscinus semoni*), with B.M. 99.10.24.1, a female, also from Queensland and with B.M. 50.1154-1155, a male and female from the Buntibasa district, Kratke Mountains, Northeast New Guinea. The collections of the British Museum (Natural History) also contain a specimen from Avera, Aroa River, Papua, B.M. 4.4.11.4, with only the rostrum and mandible remaining of the skull, which must be referred to this species. Tate, who thus studied *H. semoni* in the mistaken belief that he had before him specimens of *H. muscinus*, thus came to the logical conclusion that *H. muscinus* and *H. semoni* were conspecific. Furthermore, he wrote (1941 : 379) "Dahl and Collett, both of whom wrote in 1897, evidently had North Australian material, which they alluded to as *muscinus*". However, at that time neither *H. semoni* nor *H. stenotis* had been described, and Tate was apparently unaware that one of the specimens collected by Dahl at the Mary River, Northern Territory, Australia and referred by Dahl (1897 : 191) and Collett (1897 : 320) to *H. muscinus* was received by the British Museum (Natural History) in exchange with the then Christiania Museum in 1897 and subsequently became the type specimen of *H. stenotis*.

For the present, *H. semoni* and *H. stenotis* are treated as distinct species, although their differences are those of degree rather than of structure. *Hipposideros stenotis*, however, is a much smaller bat than *H. semoni*, and has the protuberances of the intermediate leaf and especially the posterior leaf less greatly developed. The frontal depression is more greatly excavated than in *H. semoni* and its rostral eminences are less inflated, while its anteorbital foramen is larger in relation to the size of its skull. The teeth of *H. stenotis* are smaller and less massive than those of *H. semoni*. The anterior upper premolar (pm^2) in *H. stenotis* is absent : in *H. semoni* this tooth is absent in the type (Thomas (1913b : 206)) but is present in both sides of the jaw of all the specimens of *H. semoni* examined during the preparation of these notes.

Relationships within the group are summarized in Figure 19. The *muscinus* group evidently originates from within the *bicolor* group or from the *bicolor-speoris* stem and some of its features are incipiently displayed by *H. papua*, a species remotely allied to *H. bicolor* and its allies. The *muscinus* group is isolated within *Hipposideros* by the highly modified characters of its ears, noseleaves and auditory region, which are specialized to an extent otherwise nowhere approached in this

large genus. Its extremely discontinuous distribution and the complexity of its characters suggest a relict group of remote origin, a view supported by the profound differences between its Ethiopian representatives and its remaining representatives in the Australasian region.

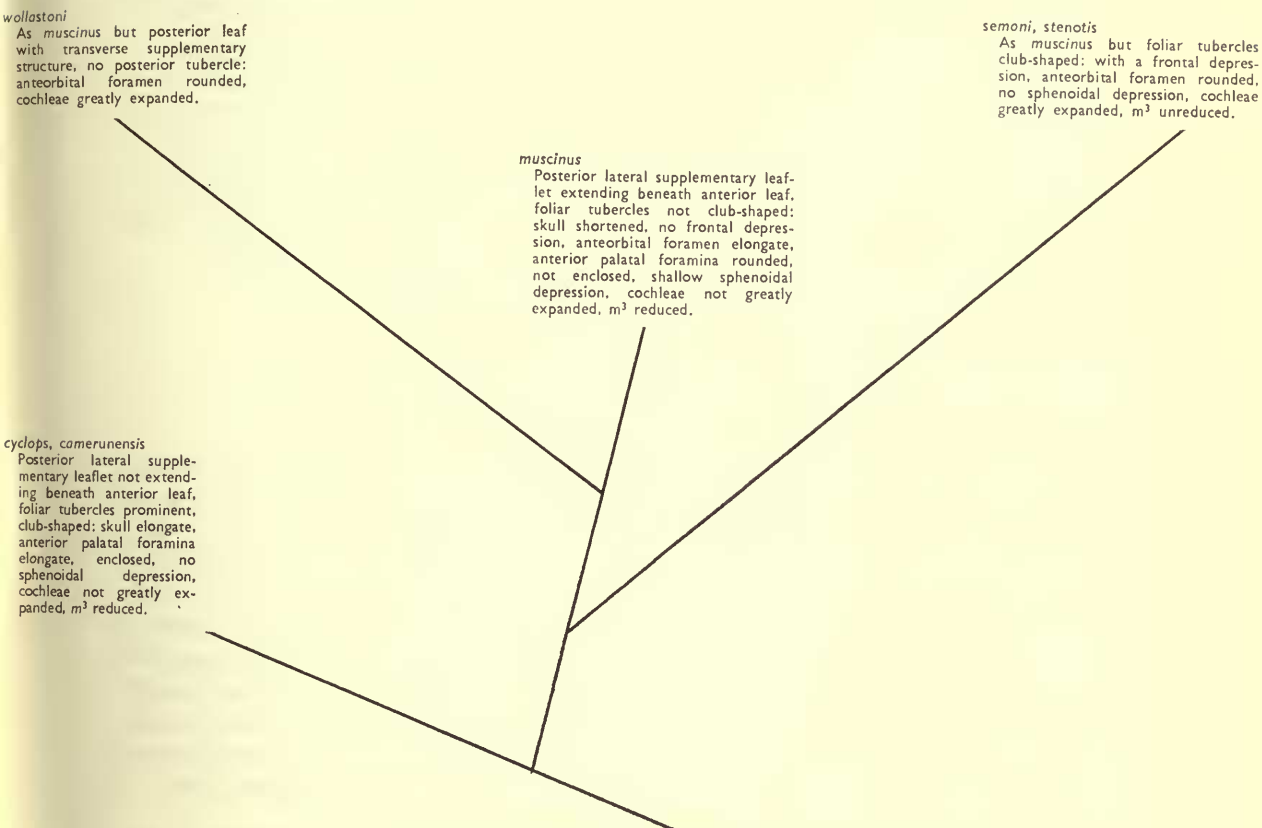


FIG. 19. Possible relationships in the *Hipposideros muscinus* group

The species of the *cyclops* group may be keyed :

- 1 Posterior lateral supplementary leaflet not extending anteriorly beneath the anterior leaf : premaxillae wide, enclosing the anterior palatal foramina, making a broad junction with the maxillae 2
- Posterior lateral supplementary leaflet extending anteriorly beneath the anterior leaf : premaxillae narrow, not enclosing the anterior palatal foramina, making a narrow, spatulate junction with the maxillae 3
- 2 Smaller, length of forearm less than 74.0 mm.: anteorbital foramen relatively large *cyclops* (p. 78)
- Larger, length of forearm exceeding 74.0 mm.: anteorbital foramen relatively small *camerunensis* (p. 80)
- 3 Median process of intermediate leaf not greatly developed or club-shaped : frontal depression absent, shallow sphenoidal depression present, posterior ridge of m^3 reduced, W-pattern of tooth incomplete 4

- Median process of intermediate leaf well developed, club-shaped : frontal depression present, sphenoidal depression absent, posterior ridge of m^3 little reduced, W-pattern of tooth almost complete 5
- 4 Posterior leaf with a median process and without a transverse supplementary structure developed from its posterior face : width of cochleae four to five times their distance apart *muscinus* (p. 81)
- Posterior leaf without a median process and with a transverse supplementary structure developed from its posterior face : width of cochleae six or more times their distance apart *wollastoni* (p. 83)
- 5 Median process of posterior leaf well developed : frontal depression shallow, rostral eminences greatly inflated, anteorbital foramen relatively small *semoni* (p. 84)
- Median process of posterior leaf not greatly developed : frontal depression deep, rostral eminences moderately inflated, anteorbital foramen relatively large *stenotis* (p. 86)

Hipposideros cyclops (Temminck)

(Figure 20)

Phyllorhina cyclops Temminck, 1853 : 75. River Boutry, Ghana.

Rhinolophus micaceus De Winton, 1897 : 524. Como River, 75 miles from Gaboon.

Hipposideros langi J. A. Allen, 1917 : 434. Avakubi, eastern Congo.

The ears are exceptionally long and narrow, their posterior margins with a concavity behind the tip and without antitragal modification. The noseleaf is large, with two lateral supplementary leaflets. The anterior leaflet is short but wide : the posterior leaflet extends upwards to join the base of the posterior leaf but does not extend anteriorly beneath the anterior leaf. The anterior leaf has no median emargination, the internarial septum is not greatly inflated and the narial lappets are slightly expanded. The intermediate part of the leaf is flat but is specialized by the development of a median club-like process. The posterior leaf is moderately high, its upper edge more or less semicircular, thickened but not lobulated, and is supported by three septa enclosing deep pockets. It is specialized by the development of a median club-like process from the upper part of its anterior face. A frontal sac is present in both sexes.

The skull is large and elongate, with an elongate braincase and low sagittal crest. The interorbital region is rather constricted but not greatly shortened, and the supraorbital ridges are well defined. There is a moderate frontal depression and the rostral eminences are moderately inflated, separated by a shallow groove. The zygomata are comparatively massive, with a low jugal projection. The anteorbital foramen is large and rounded, closed by a moderate bar of bone. The premaxillae are broad, together almost filling the anterior palatal emargination, and wholly enclose the anterior palatal foramina. They are very wide posteriorly and make a broad, shallowly V-shaped junction with the maxillae. The palate is short, with a square palation. The mesopterygoid fossa is moderate, with the vomer projecting very slightly, and the pterygoids are long, with the sphenoidal bridge only very slightly constricted, almost completely concealing narrow, elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are large, their width equal to four times their distance apart. The upper incisors are

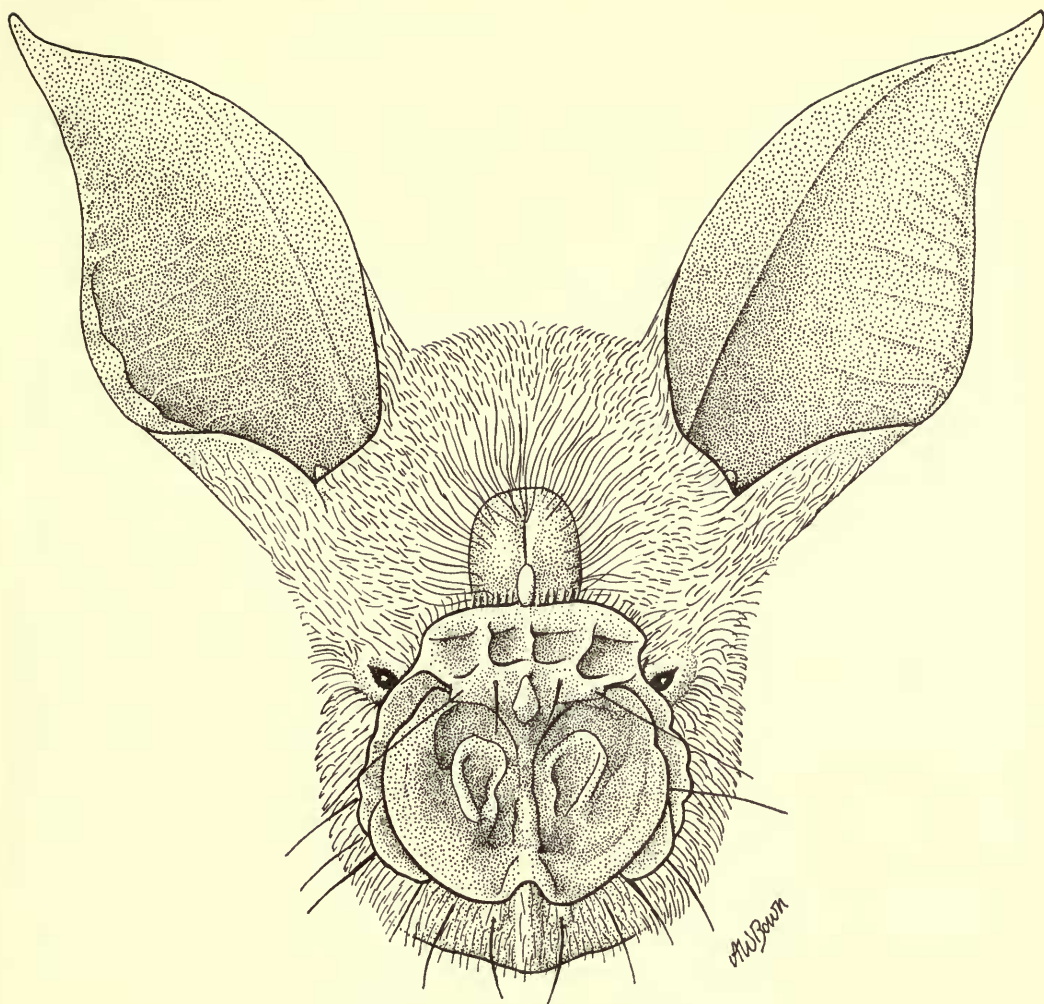


FIG. 20. *Hipposideros cyclops* ♂ (B.M. 30.11.11.151) (x3)

very weakly bilobed, and the upper canines lack cusps but have prominent cingula. The anterior upper premolar (pm^2) is not greatly reduced but is extruded from the toothrow with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors is equal to or slightly exceeds the crown area of the inner pair and the anterior lower premolar (pm_2) is much reduced, one quarter the length and one half the height of the second lower premolar (pm_4). Hayman (1935) gives an account of *H. cyclops*.

DISTRIBUTION : Portuguese Guinea (Veiga Ferreira (1949 : 1951)) ; Sierra Leone ; Liberia ; Ghana ; Nigeria ; Cameroons ; Congo ; Kenya ; Uganda.

Hipposideros camerunensis Eisentraut

Hipposideros camerunensis Eisentraut, 1956 : 526. Buea, Cameroons.

The ears and noseleaf of *H. camerunensis* closely resemble those of *H. cyclops* but the ears of *H. camerunensis* are rather larger and the noseleaf is broader than in this species. A frontal sac is present in both sexes. The skull is similar to that of *H. cyclops* and is long and rather elongate, with a broadened braincase and low sagittal crest. The interorbital region is sharply constricted with well-defined supraorbital ridges. There is a moderate frontal depression and the rostrum is expanded and broad, with moderately inflated rostral eminences separated by a shallow groove. The zygomata are massive, with a moderate jugal projection. The anteorbital foramen is comparatively small, closed by a narrow bar of bone. The premaxillae are broad, like those of *H. cyclops*, together almost filling the anterior palatal emargination, and wholly enclose the elongate anterior palatal foramina. As in *H. cyclops*, they are wide posteriorly, and make a broad, shallowly V-shaped junction with the maxillae. The palate is short and the palation almost square. The mesopterygoid fossa is moderate, the vomer projecting very slightly, and the pterygoids are long with the sphenoidal bridge only slightly constricted and almost concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are large as in *H. cyclops*, their width equal to four times their distance apart. The dentition almost exactly resembles that of *H. cyclops*. The upper incisors are weakly bilobed, the upper canines lack cusps and the anterior upper premolar (pm^2) is not greatly reduced, extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors slightly exceeds the crown area of the inner pair and the anterior lower premolar (pm_2) is one quarter the length and one half or slightly less the height of the second lower premolar (pm_4).

Hipposideros camerunensis is closely related to *H. cyclops* and differs from this species in its larger size, broader skull with broader braincase and rostrum and

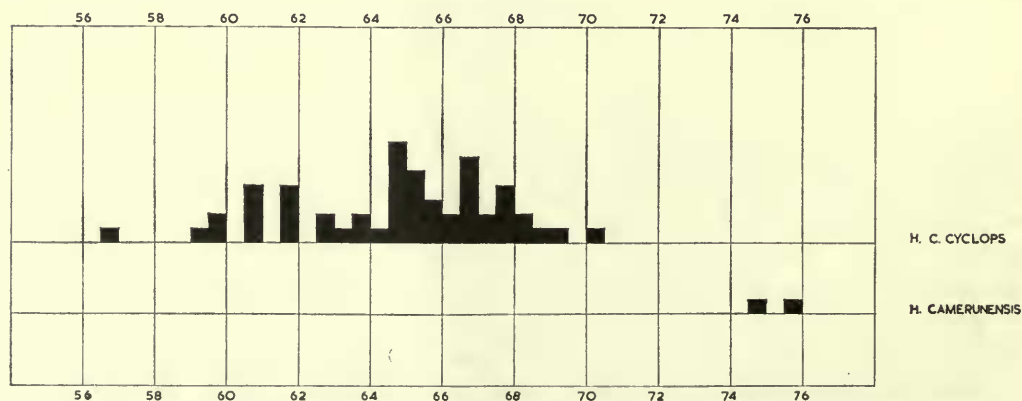


FIG. 21. Length of forearm in *Hipposideros cyclops* and *H. camerunensis*

smaller anteorbital foramen. The two species are the most primitive of the *cyclops* group, with their skulls elongate and not markedly shortened as in *H. muscinus* and its allies. Nevertheless, they display the specializations of the group to a considerable degree, notably in the elongation of their ears, the development of foliar prominences and the enlargement of their cochleae. Eisentraut (1963 : 87) discusses the status of *H. camerunensis* and records further specimens from Buea, Cameroons.

DISTRIBUTION : Cameroons ; Congo (first record : specimen from Shabunda, eastern Congo, in collection of British Museum (Natural History)).

***Hipposideros muscinus* (Thomas & Doria)**

(Figure 22)

Phyllorhina muscina Thomas & Doria, 1886 : 201, 1 fig. Fly River, Papua.

The ears are very long and comparatively narrow, although not excessively so, with their posterior margins slightly concave behind the tip. They lack any anti-tragal modification and are largely naked. The noseleaf is large, with two lateral supplementary leaflets. The anterior leaflet is short and broad, projecting widely beyond the lateral margin of the anterior leaf. The posterior leaflet is broad and extends posteriorly to join the posterior leaf and anteriorly beneath the anterior leaf on to the upper lip. The anterior leaf has no median emargination and the internarial septum is slightly swollen, especially anteriorly. The narial lappets are well developed, but the nostrils are only slightly pocketed. The intermediate part of the leaf is very slightly inflated with a small median tubercle-like process. The posterior leaf is high, its upper edge flattened, thickened and with a small median

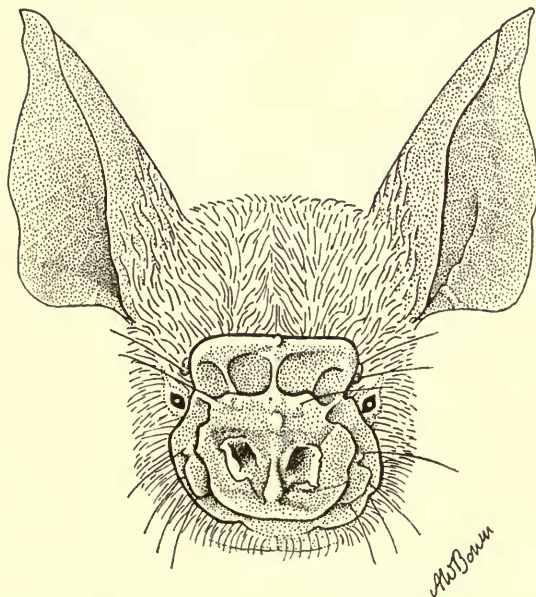


FIG. 22. *Hipposideros muscinus* ♀ (Syntype B.M. 86.11.3.10) (x3)

projecting tubercle. The posterior leaf is supported by three septa enclosing shallow pockets.

The skull is small, short and broad, with a low sagittal crest. The interorbital region is short and sharply constricted, the supraorbital ridges well defined. There is no frontal depression and the rostral eminences are moderately inflated, separated by a shallow groove. The zygomata are slender, with a low jugal projection and the anteorbital foramen is small, elongate and closed by a narrow bar. The junction of the premaxillae with the palate is U-shaped: the palate is very short with a U-shaped palation. The mesopterygoid fossa is wide, the pterygoids long and wide and the sphenoidal bridge barely constricted, partially concealing elongate lateral apertures. There is a shallow sphenoidal depression bisected by a low median ridge. The cochleae are large, their width equal to four or five times their distance apart. The upper canines are slender, without cusps, and the anterior upper premolar (pm^2) is not excessively reduced and is only slightly out of alignment in the toothrow, separating the canine and the second upper premolar (pm^4). The posterior ridge of the third upper molar is obsolescent, its length less than one quarter the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than the crown area of the inner pair and the anterior lower premolar (pm_2) is one third the length and height of the second lower premolar (pm_4).

Although the only specimen available for study is the syntype, there is no reason to consider that *H. muscinus* is conspecific with either *H. semoni* or *H. stenotis*. *Hipposideros muscinus* has ears shorter and broader than in these species, and has the projecting processes of the intermediate and posterior noseleaves less developed. Cranially, it differs quite markedly from either, with more sharply defined supraorbital ridges and a wider rostrum, the rostral eminences less inflated, the rostrum from its lateral aspect horizontal above, lacking the marked concavity over the interorbital region separating the rostral eminences and braincase in *H. semoni* and *H. stenotis* and lacking the frontal depression found in these species. In *H. muscinus* the anteorbital foramen is small and elongate, in contrast to the rounded foramina of *H. semoni* and *H. stenotis*: the sphenoidal bridge of *H. muscinus* is wider than in these species and a sphenoidal depression, absent in both, is present in *H. muscinus*. Its cochleae are less expanded than those of *H. semoni* or *H. stenotis* and the angular and articular processes of the mandible are not markedly connected by a thin web of bone as in these species. The third upper molar of *H. muscinus* has its posterior ridge greatly reduced and almost obsolete, contrary to the condition evident in *H. semoni* and *H. stenotis*, which have the posterior ridge of this tooth nearly equal in length to the anterior ridge and almost entire. These considerations indicate that while *H. muscinus* without doubt is allied to *H. semoni* and *H. stenotis*, it can by no means be considered conspecific with either of these species. It is less specialized than either *H. semoni* or *H. stenotis*, and cranially is similar to *H. wollastoni*. This species, however, differs from *H. muscinus* in the development of a transverse supplementary structure from the posterior face of the posterior leaf, in more inflated rostral eminences (similar in fact to those of *H. semoni* and *H. stenotis*) and in a greater degree of expansion of the cochleae.

Hipposideros wollastoni Thomas

Hipposideros wollastoni Thomas, 1913b : 205. Camp 3, Utakwa River, southwestern Netherlands New Guinea.

The ears are long and comparatively narrow, pointed, their posterior margins slightly concave behind the tip. They lack antitragal modification and are largely naked. The noseleaf is large with two lateral supplementary leaflets exactly similar to those of *H. muscinus*. The anterior leaf resembles that of *H. muscinus* but the internarial septum is slightly more inflated and the nostrils are slightly pocketed. The intermediate leaf is not inflated but has a large projecting median eminence. The upper edge of the intermediate part of the leaf is elevated laterally, these elevations forming a base for and largely concealing the lateral supporting septa of the posterior leaf. The posterior leaf has its upper edge semicircular, unthickened and lacking a median projection, and is supported by three septa enclosing shallow pockets. A transverse supplementary structure with a serrate upper edge is developed from its posterior face, and is equal in height almost to the posterior leaf. This structure is joined longitudinally to the posterior leaf by two external and two intermediate septa, enclosing three small pockets. A wart-like eminence arises on each side of the muzzle just behind the posterior leaf. There is a small depression but no frontal sac in the female type specimen.

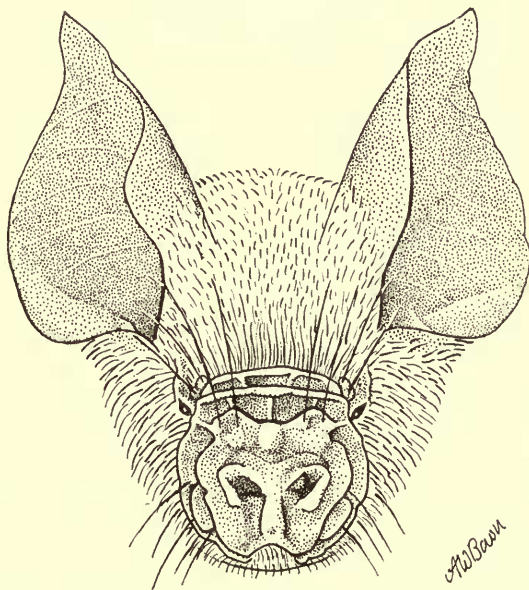


FIG. 23. *Hipposideros wollastoni* ♀ (Type B.M. 13.6.18.4) (x3)

The skull in general outline is very like that of *H. muscinus*, with a moderate sagittal crest and a constricted interorbital region. The supraorbital ridges are evident but not sharply defined, especially behind the rostral eminences. There is

no frontal depression and the rostral eminences are considerably inflated, separated by a deep groove, and give the rostrum from its lateral aspect a marked elevation. The zygomata are slender, with a moderate jugal projection while the anteorbital foramen is small, rather rounded and closed by a narrow bar. The premaxillae are narrow, spatulate posteriorly, and make a narrow junction with the maxillae. They do not enclose the rounded anterior palatal foramina, the anterior walls of which are formed by the delicate anterior enclosing processes of the premaxillae. The palate is short and the palation U-shaped with a small post-palatal spicule. The mesopterygoid fossa is wide and the pterygoids are long, with an almost unstricted sphenoidal bridge, partially concealing elongate lateral apertures. There is a small sphenoidal depression, lacking any median ridge. The cochleae are greatly expanded, their width equal to six times their distance apart. The angular and articular processes of the mandible are not markedly connected by a web of bone. The upper incisors are not bilobed and the upper canines lack cusps, while the anterior upper premolar (pm^2) is small and extruded, the canine and the second upper premolar (pm^4) almost in contact. The posterior ridge of the third upper molar is equal in length to one third of the length of the anterior ridge, the W-pattern of the tooth incomplete. The crown area of the outer lower incisors is slightly greater than that of the inner pair, and the anterior lower premolar (pm_2) is a little under one half the length and height of the second lower premolar (pm_4).

Despite its specialized noseleaf, *H. wollastoni* is more closely related to *H. muscinus* than to *H. semoni* or *H. stenotis*. Its ears, which are more acutely pointed than those of *H. muscinus* but shorter and broader than those of *H. semoni* or *H. stenotis*, its more advanced noseleaf, broader, more inflated rostrum and more greatly expanded cochleae show *H. wollastoni* to be a more specialized bat than *H. muscinus*.

***Hipposideros semoni* Matschie**

(Figure 24)

Hipposideros semoni Matschie, 1903 : 774 (Heft 6 : 132). Cooktown, northern Queensland.

The ears are very long and narrow, with an acute, narrow point. Their posterior margins are markedly concave just behind the tip, they lack any antitragal modification and are haired for one third of their length. The noseleaf is a highly developed structure covering much of the muzzle, and has two lateral supplementary leaflets. The anterior leaflet is short and broad, projecting widely beyond the lateral margin of the anterior leaf as in *H. muscinus* and *H. wollastoni*. As in these species, the posterior leaflet extends posteriorly to become continuous with the posterior leaf and anteriorly beneath the anterior leaf. The anterior leaf has no median emargination and the internarial septum is slightly inflated with the narial lappets well developed, the nostrils not pocketed. The intermediate part of the leaf is flat, its upper edge elevated laterally and bears a very well-developed club-shaped projection. The posterior leaf is high, supported by three septa, its upper edge semicircular, with a well-developed median club-shaped projection.

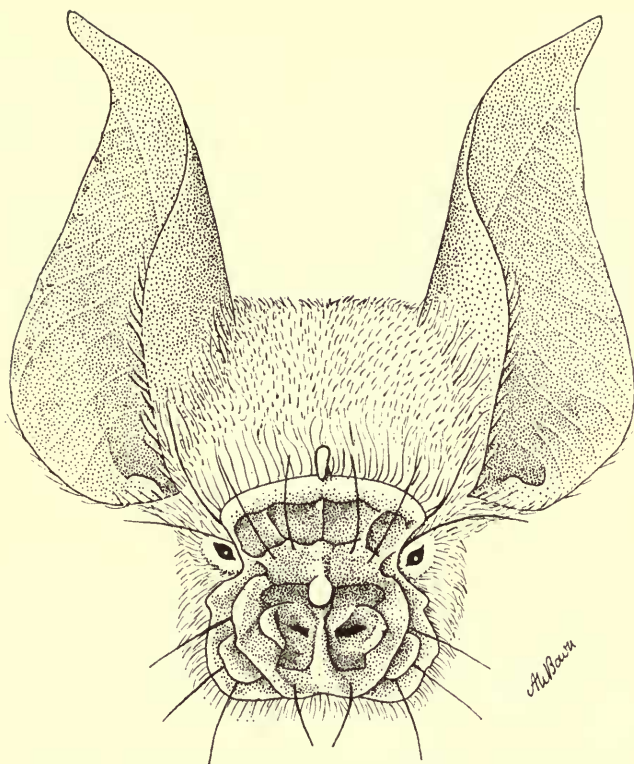


FIG. 24. *Hipposideros semoni* ♀ (B.M. 99.10.24.1) (x3)

The skull is short and broad, with a broad braincase and prominent sagittal crest. The interorbital region is moderately constricted with prominent supraorbital ridges which are less developed behind the rostral eminences. There is a shallow frontal depression and the rostral eminences are greatly inflated, to give the rostrum from its lateral aspect a much elevated appearance, deeply concave above the interorbital region. The zygomata are moderate, with a low jugal process and the anteorbital foramen is small and round, separated by a narrow bar. The premaxillae are much as in *H. wollastoni*, narrow, spatulate posteriorly and making a narrow junction with the maxillae. They do not enclose the rounded anterior palatal foramina. The palate is short, the palation square with a post-palatal spicule. The mesopterygoid fossa is wide while the pterygoids are long and the sphenoidal bridge moderately constricted, exposing elongate lateral apertures. There is no sphenoidal depression, but the sphenoidal region is traversed by a low longitudinal ridge. The cochleae are enormous, their width equal to eight times their distance apart, almost touching, separated by a very narrow basioccipital. The angular and articular processes of the mandible are united by a thin web of bone. The upper incisors are weakly bilobed, the upper canines without cusps and the anterior upper premolar (pm²) very small, extruded from the toothrow, with the canine and the second upper premolar (pm⁴) in contact: Thomas (1913b: 206) notes that this

tooth is absent in the type specimen. The posterior ridge of the third upper molar is not greatly reduced, its length equal to two thirds the length of the anterior ridge and with the W-pattern of the tooth almost complete. The crown area of the outer lower incisors is slightly greater than that of the inner pair and the anterior lower premolar (pm_2) is less than one quarter the length and height of the second lower premolar (pm_4).

Hipposideros semoni is clearly quite distinct from *H. muscinus*, differing from this species in a number of salient features, among which the greater development of the ears and noseleaf, rostrum and cochleae are the most important. It is patently one of the most, if not the most specialized species of the *cyclops* group and together with the closely related *H. stenotis* represents the culmination of a line of specialization of which *H. papua* is perhaps an offshoot and *H. muscinus* a later development.

DISTRIBUTION : Northern Australia ; Papua ; Northeast New Guinea.

Hipposideros stenotis Thomas (Figure 25)

Hipposideros stenotis Thomas, 1913b : 206. Mary River, Northern Territory, Australia.

Externally, *H. stenotis* is closely similar to *H. semoni* but is considerably smaller. The ears are exactly as described for that species, while the noseleaf almost exactly resembles that of *H. semoni* except that the median projection of the posterior leaf is less prominent. The skull is short and broad, with moderate sagittal crest and supraorbital ridges like those of *H. semoni*. There is a deep frontal depression and the rostral eminences are moderately inflated, sufficiently that the rostrum from its lateral aspect appears elevated. The zygomata are slender, with a low jugal projection and the anteorbital foramen is rounded, closed by a narrow bar. The premaxillae are similar to those of *H. wollastoni* and *H. semoni*, spatulate posteriorly, making a narrow junction with the maxillae and not enclosing the rounded anterior palatal foramina. The palate is short and the palation square, with a small post-palatal spicule. The mesopterygoid fossa is moderate, the pterygoids long and the sphenoidal bridge moderately constricted exposing wide, elongated lateral apertures. There is no sphenoidal depression and the sphenoidal region is traversed by a low longitudinal ridge. The cochleae are enormous, their width equal to eight times their distance apart, almost touching, separated by a very narrow basioccipital. The angular and articular processes of the mandible are connected by a web of bone. The upper incisors are weak and not bilobed : the type specimen is unusual in that a second right hand upper incisor is present. It is a peg-like tooth, longer but more slender than the first upper incisor. The upper canines lack cusps and the anterior upper premolar (pm^2) is absent, with the canine and the second upper premolar (pm^4) in contact. The posterior ridge of the third upper molar is not greatly reduced and is two thirds the length of the anterior ridge, with the W-pattern of the tooth almost complete. The crown area of the outer lower incisors is a little greater than that of the inner pair and the anterior lower premolar (pm_2) is much reduced, one quarter the length and height of the second lower premolar (pm_4).

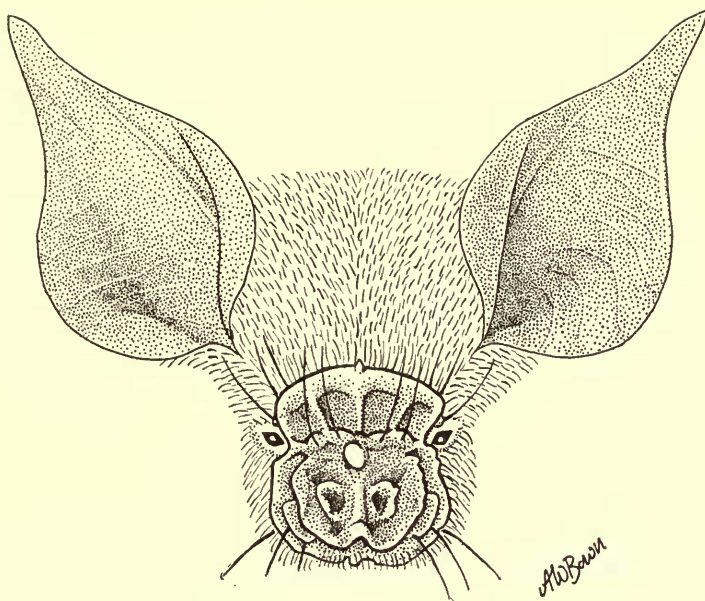


FIG. 25. *Hipposideros stenotis* ♀ (Type B.M. 97.4.12.7) (x3)

Although the close structural similarity of *H. stenotis* to *H. semoni* suggests that the two may be conspecific, there is considerable disparity in size and *H. stenotis* has the protuberances of its intermediate and posterior noseleaves less developed. Cranially, its frontal depression is deeper than that of *H. semoni* and its rostral eminences less inflated: its anteorbital foramen is larger and the molars much less massive. Only the type specimen of *H. stenotis* is available for study and for the present it is retained as a distinct species. Tate (1941: 389) records a series of *H. stenotis* from Papua in the collections of the American Museum of Natural History. Despite careful search by the authorities of that Museum, no trace of this series has been found.

HIPPOSIDEROS PRATTI group

This group contains only two species, *H. pratti* and *H. lylei*, both Asiatic in distribution. The ears are large and broad, bluntly pointed with their posterior margins slightly concave behind the tip. They lack antitragal modification and are haired for one third of their length. The noseleaf has two lateral supplementary leaflets and the anterior leaf a median emargination. The intermediate part of the leaf is expanded, with a median eminence and the posterior leaf is high in the centre, triangular, supported by a prominent median ridge flanked by two much weaker ridges. The group is noteworthy for the development of transverse fleshy lobate prominences on each side of the opening of the frontal sac to form a structure resembling a supplementary posterior noseleaf traversing the muzzle behind the true posterior leaf. The degree of development of this structure varies considerably, but is always at its greatest in male specimens.

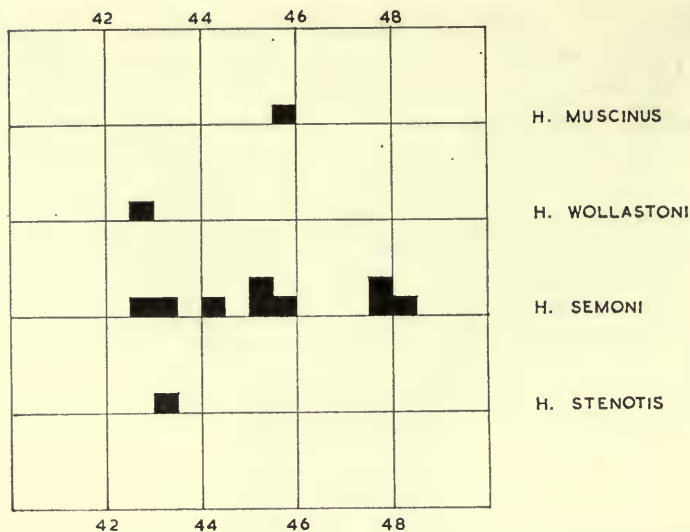


FIG. 26. Length of forearm in *Hipposideros muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis*

The skull is of moderate to large size, with a moderate sagittal crest. The inter-orbital region is short, with well-defined supraorbital ridges and there is a shallow frontal depression. The rostrum is low and broad with moderately inflated rostral eminences. The zygomata are slender and have a moderate jugal projection, while the anteorbital foramen is rounded and closed by a narrow bar. The premaxillae make a fan-shaped junction with the maxillae and totally enclose the rounded anterior palatal foramina. The palate is short and wide, the pterygoids comparatively short and the sphenoidal bridge not markedly constricted. There is a well-defined sphenoidal depression and the cochleae are small, their width equal to or less than their distance apart. The outer lobe of the upper incisors is only slightly smaller than the inner lobe, and the anterior upper premolar (pm^2) is reduced, extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is almost obsolete. The crown area of the outer lower incisors is greater than that of the inner pair, and the anterior lower premolar is one half the length and height of the second lower premolar (pm_4).

Although Ellerman & Morrison-Scott (1951 : 129) considered *H. pratti* and *H. lylei* to be conspecific, the two evidently are widely separated by differences in the structure of the noseleaf and cranial architecture which in no way support the view that they are conspecific. Their taxonomic position within the genus is not easy to determine. The presence of two lateral supplementary leaflets and their short, broadened skulls recalls the more specialized species of the *bicolor* group while the development of a supplementary lobate structure behind the posterior leaf in both forms and the presence of an abrupt discontinuity between the roofs of the meso-ptyergoid and narial canals in *H. pratti* suggest an affinity with the *armiger* group.

The depressed rostrum and the presence of a frontal depression in the *pratti* group, however, render close alliance with the *armiger* group unlikely. In the present work, the *pratti* group is regarded as linking bats of the *bicolor* group to the more specialized bats of the *armiger* group, displaying no affinities towards either the *speoris* or *diadema* groups.

The two species of the *pratti* group may be keyed :

- i Lateral margins of anterior leaf not continuous with those of posterior leaf : rostrum lacking lateral pits, an abrupt step-like discontinuity between roofs of narial and mesopterygoid canals, vomer projecting posteriorly beyond palate *pratti* (p. 89)
- Lateral margins of anterior and posterior leaves continuous : rostrum with lateral pits, roofs of narial and mesopterygoid canals merging smoothly, vomer not projecting posteriorly beyond palate *lylei* (p. 90)

Hipposideros pratti Thomas

Hipposiderus (sic) *pratti* Thomas, 1891 : 527. Kiatingfu, Szechuan, China.

The ears and noseleaf agree closely with the group description. The anterior leaf has a single median emargination and its lateral margins are not continuous with those of the posterior leaf. The internarial septum is uninflated and the narial lappets moderately developed. The intermediate part of the leaf is inflated with a prominent median eminence. Its upper edge is elevated laterally to form a large transverse structure across the noseleaf anterior to the lower part of the posterior leaf. The posterior leaf is more or less triangular in outline and is supported by a well-defined median septum, flanked laterally by weaker ridges, barely enclosing small cells. Two large lobate projections are developed transversely behind the posterior leaf, one each side of the opening of the frontal sac, to form an enlarged supplementary transverse structure, the projections separated by a deep median notch at the aperture of the sac. A small tuft of bristle-like hairs projects through this notch. This transverse structure is more greatly developed in old male animals than in young male or female examples. A frontal sac is present in both sexes.

The skull is large and broad, with a well-developed sagittal crest. The interorbital region is markedly constricted and there are prominent supraorbital ridges. There is a shallow frontal depression and the rostrum is broad, its upper surface below the level of that of the braincase, bluntly angular, with a pentagonal outline and with the rostral eminences not greatly inflated. The zygomata and the anteorbital foramen are as described for the group as are the premaxillae, which make a U-shaped junction with the maxillae. The palation is U-shaped and the mesopterygoid fossa wide with the posterior part of the narial canal deeply excavated, an abrupt step-like discontinuity separating its roof from the roof of the mesopterygoid fossa. The vomer is thin and blade-like, projecting posteriorly beyond the edge of the palate. The pterygoids are moderate and the sphenoidal bridge constricted, exposing wide, elongate apertures. The sphenoidal depression, cochleae and dentition are as described for the group. Osgood (1932 : 222) gives detailed illustrated notes on specimens from Tonkin.

Pohle (1943 : 323) considers a specimen in the Berlin Museum to be the holotype of *Phyllorhina swinhoii* Peters (in Swinhoe, Proc. zool. Soc. Lond. 1870 (1871) : 616) (more correctly *swinhoei*) and has suggested that *H. pratti* is synonymous with the species described by Peters. However, Peters (1871a : 317) considered *H. swinhoei* to be a synonym of *H. armiger* (Hodgson) and was followed in this opinion by Dobson (1878 : 135) and Andersen (1906a : 37) while Tate (1941 : 371, 389) who had available a photograph "of the type skull", a topotype from Amoy and other specimens from China, considered *H. swinhoei* to be a subspecies of *H. armiger*. There are three specimens from the original series collected by Swinhoe in the collections of the British Museum (Natural History). All have three lateral supplementary leaflets and cannot therefore be regarded as *H. pratti*. In the present work *H. swinhoei* (Peters) is regarded as a synonym of *H. armiger armiger* (Hodgson).

DISTRIBUTION : Southwestern China ; Indochina : Tonkin.

Hipposideros lylei Thomas

Hipposideros lylei Thomas, 1913a : 88. Chiendao Cave, 50 miles north of Chiangmai, Siam, 350 metres.

The ears are broad and triangular, slightly less acutely pointed than in *H. pratti*, their posterior margins shallowly concave behind the tip and slightly thickened at the antitragal lobe. The noseleaf in its essentials resembles that of *H. pratti*, with two small lateral supplementary leaflets, but is slightly more specialized. The anterior leaf projects forward over the upper lip and has a deep median emargination, the edge of the leaf lateral to this emargination shallowly emarginated on each side to form two small projecting lappets. Its lateral margins are continuous with those of the posterior leaf but are separated from them at the level of the intermediate part of the leaf by a shallow notch on each side. The internarial septum is not greatly inflated and the narial lappets are well developed. The intermediate part of the leaf is similar to that of *H. pratti* and has a well-developed median eminence. Its lateral margins are embellished on each side with a small outwardly projecting lappet at the level of the notches in the lateral margins of the anterior and posterior leaves. The posterior leaf is triangular in outline and is supported by a median septum and two weaker lateral ridges. There is a greatly developed transverse supplementary structure behind the posterior leaf as described for *H. pratti*.

The skull is of moderate to large size, with a low sagittal crest. The interorbital region is markedly constricted and the interorbital ridges are sharply defined. There is a well-developed frontal depression and the rostrum is broad, low as in *H. pratti*, with the rostral eminences slightly inflated. There is a lateral depression on each side of the rostrum immediately above the anteorbital foramen : these depressions are a little deeper than the frontal depression. The zygomata are moderate with a moderate jugal process and the anteorbital foramen, premaxillae and palate are as described for the group, the premaxillae making a broad, U-shaped junction with the maxillae and the palation more acute, almost V-shaped. The

mesopterygoid fossa is wide, and the roof of the narial canal, although discontinuous with the roof of the mesopterygoid canal, merges into it smoothly, without an abrupt, step-like discontinuity. The vomer does not project posteriorly beyond the edge of the palate. The pterygoids are short and wide, the sphenoidal bridge less constricted than in *H. pratti*, partially concealing elongate lateral apertures. The sphenoidal depression, cochleae and dentition are as described for the group.

Hipposideros lylei differs from *H. pratti* in the deeper median emargination of its anterior leaf, flanked by two shallow lateral emarginations absent in *H. pratti*: in the continuity of the lateral margins of the anterior and posterior noseleaves, which are separated only by lateral marginal notches and in the presence of small lateral lappets at the margins of the intermediate part of the leaf. It has a deeper frontal depression: lateral rostral pits, present in *H. lylei*, are absent in *H. pratti* and the zygomata of *H. lylei* are more massive than those of *H. pratti*. In *H. lylei* the roofs of the narial and mesopterygoid canals merge smoothly, without the abrupt, step-like discontinuity characteristic of *H. pratti* and the sphenoidal bridge of *H. lylei* is wider than that of *H. pratti*, partially concealing the lateral apertures.

DISTRIBUTION: Burma; North Shan States; Siam; Federation of Malaya.

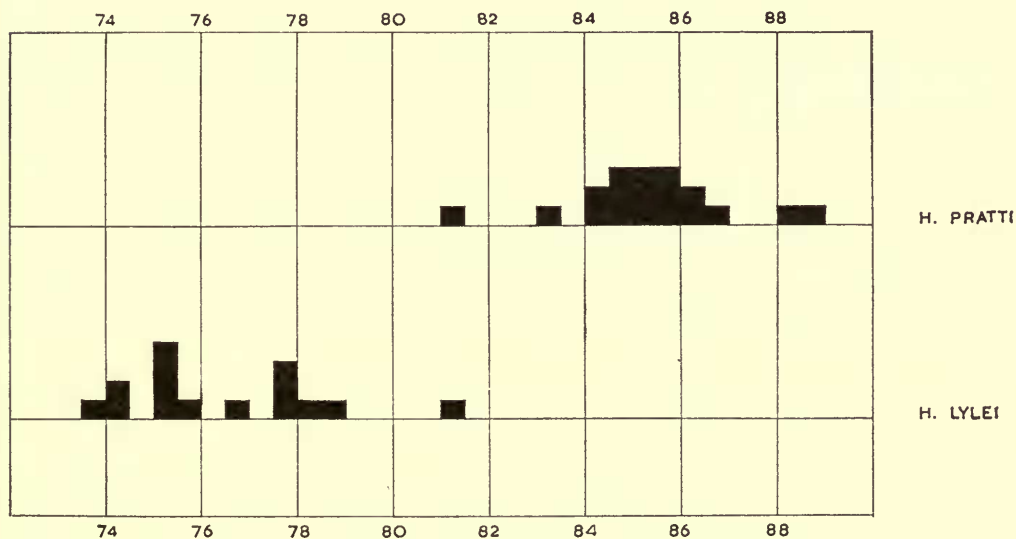


FIG. 27. Length of forearm in *Hipposideros pratti* and *H. lylei*

HIPPOSIDEROS ARMIGER group

The ears are large, broad and acutely pointed, their posterior margins concave behind the tip. They are slightly thickened at the antitragal lobe and are haired for one third of their length. The noseleaf is broad, with four supplementary leaflets, the fourth small, sometimes rudimentary. The anterior leaf has no distinct median notch, the internarial septum is not inflated and the narial lappets are not greatly

developed. The intermediate part of the leaf is slightly inflated with a prominent median eminence. The posterior leaf is high and narrow, not as wide as the anterior leaf, its upper edge flattened, thickened, becoming trilobate and is supported by a prominent median septum and two less evident lateral septa. Prominent fleshy elevations arise behind the posterior leaf on each side above the eyes to form a transverse supplementary structure, found at its greatest development in old male specimens, less developed in young male and female examples. There is a frontal sac in male specimens : in female examples it is small or is represented by a depression.

The skull is of moderate to large size with well-developed sagittal crest, short, constricted interorbital region and sharply defined supraorbital ridges. There is no frontal depression and the rostral eminences are uninflated. The naso-frontal region is decidedly pentagonal in outline and the rostrum is elevated posteriorly, in profile forming a nearly horizontal surface on a level with the upper surface of the braincase. The zygomata are moderate to strong, with a moderate to well-developed jugal projection. The anteorbital foramen is large and rounded, closed by a very narrow bar. The premaxillae make a fan-shaped junction with the maxillae and do not enclose the elongate anterior palatal foramina. The palation is U-shaped and the mesopterygoid fossa wide, with the roof of the narial canal separated from the roof of the mesopterygoid fossa by a sharp, step-like discontinuity, the vomer projecting beyond the edge of the palate. The pterygoid wings are expanded and the sphenoidal bridge is wide, almost concealing elongate lateral apertures. There is a moderate sphenoidal depression and the cochleae are small, their width less than their distance apart. The upper incisors are bilobed with the outer lobe approximately equal to the inner lobe while the upper canines have a low anterior cusp. The anterior upper premolar (pm^2) is small, extruded from the toothrow with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is greater than that of the inner pair and the anterior lower premolar (pm_2) is one third to one half the length and height of the second lower premolar (pm_4).

The *armiger* group contains two very closely related species, *H. armiger* and *H. turpis*, essentially identical in their structural characteristics and separable only by the much smaller size of *H. turpis* as compared with *H. armiger*, a situation not unparalleled elsewhere in *Hipposideros*. The group is a specialized one not closely related to the other group of large bats of the genus *Hipposideros*, the *diadema* group, with which it was compared by Andersen (1906a : 35). Its affinities lie with the *pratti* group with which the *armiger* group shares a number of specializations in the development of lobate transverse structures behind the posterior noseleaf, broad premaxillae joined to the maxillae by a wide, fan-shaped junction, a sharp discontinuity between the roofs of the narial and mesopterygoid canals (least developed in *H. lylei*, more so in *H. pratti*, *H. armiger* and *H. turpis*) and small cochleae. The *armiger* group, although having the transverse lobes behind the noseleaf less developed than in the *pratti* group, seems nevertheless slightly more specialized with a shorter, less elongate skull, no frontal depression, a high rostrum

level with the upper surface of the braincase and with the canine-bearing parts of the maxillae not prolonged anteriorly. The *armiger* group seems to have developed from the *speoris-diadema* stem, to which it is linked by the *pratti* group.

Hipposideros armiger

Size large, otherwise characters as in the group diagnosis.

DISTRIBUTION : Northern India to Formosa and the Malay Peninsula.

Hipposideros armiger armiger (Hodgson)

Rhinolophus armiger Hodgson, 1835 : 699. Nepal.

Phyllorhina swinhoii Peters, 1871b : 616. Amoy, Fukien.

Hipposideros armiger debilis Andersen, 1906a : 37. Province Wellesley, Federation of Malaya.

The status of *Phyllorhina swinhoii* Peters has been discussed in connection with *H. pratti*. The diagnosis of *H. a. debilis* Andersen rests entirely on a slightly narrower interorbital region and shorter mandibular tooththrow in Malayan specimens when compared with *H. a. armiger*. Long series in the collections of the British Museum (Natural History) do not support this contention.

DISTRIBUTION : Northern India ; Nepal ; Assam ; Burma ; southern China ; Hong Kong (Romer (1960 : 2)) ; Indochina : Tonkin (Osgood (1932 : 222)), Bourret (1942b : 11)) ; Federation of Malaya ; Langkawi Island.

Hipposideros armiger terasensis Kishida

Hipposideros armiger terasensis Kishida, 1924 : 42. Formosa.

According to Tate (1941 : 390) *H. a. terasensis* is likely to prove indistinguishable from *H. a. armiger*.

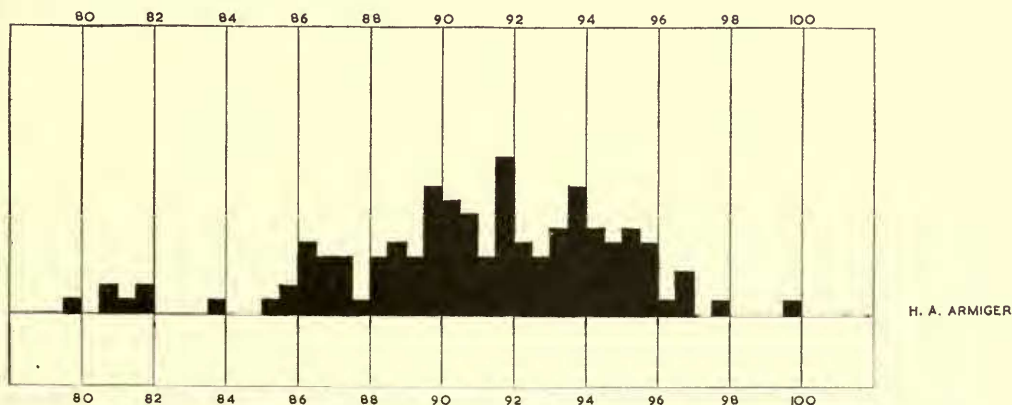


FIG. 28. Length of forearm in *Hipposideros armiger*

***Hipposideros armiger tranninhensis* Bourret**

Hipposideros tranninhensis Bourret, 1942a : 20. Plaine des Jarres, Tran-Ninh, Indochina.

From the description (repeated in part by Bourret (1942b : 12)) this form appears to be a subspecies of *H. armiger*, distinguished from *H. a. armiger* by its more trilobate posterior noseleaf.

Hipposideros turpis

The characters of this species are exactly as in *H. armiger* but it is, however, of much smaller size. The two species of the *armiger* group provide a close parallel to the situation found in some other groups of *Hipposideros* whereby two closely similar species differing chiefly in size are found to be sympatric. Such is the case with *H. galeritus* and *H. breviceps* ; *H. caffer* and *H. beatus* ; *H. cyclops* and *H. camerunensis* ; *H. lankadiva* and *H. schistaceus* and also *H. diadema* and *H. dinops*. In all of these, however, there is a small degree of structural differentiation between each pair of species : *H. armiger* and *H. turpis* are exceptional in that they differ only in size.

***Hipposideros turpis turpis* Bangs**

Hipposideros turpis Bangs, 1901 : 561. Ishigaki, South Liukiu Islands.

***Hipposideros turpis pendleburyi* Chasen**

Hipposideros pendleburyi Chasen, 1936 : 133. Near the foot of Khao Ram, Nakon Sri Tamarat, Peninsular Siam.

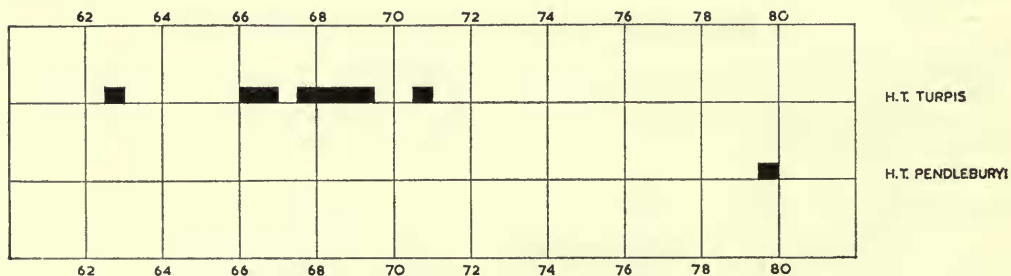


FIG. 29. Length of forearm in *Hipposideros turpis*

HIPPOSIDEROS SPEORIS group

The ears are large and comparatively broad, triangular in outline, their posterior margins concave behind the tip. Either there is a small process at the antitragal lobe or the membrane of the ear is thickened at this point. The noseleaf is simple, with three lateral supplementary leaflets. The skull is of medium size, comparatively short and with a moderate sagittal crest. The interorbital region is short and constricted and the supraorbital ridges are well developed. There is no definite frontal depression and the rostrum is low, with moderately inflated rostral eminences.

The zygomata are slender with a moderate jugal projection and the anteorbital foramen is rounded and closed by a narrow bar. The premaxillae make a wedge-

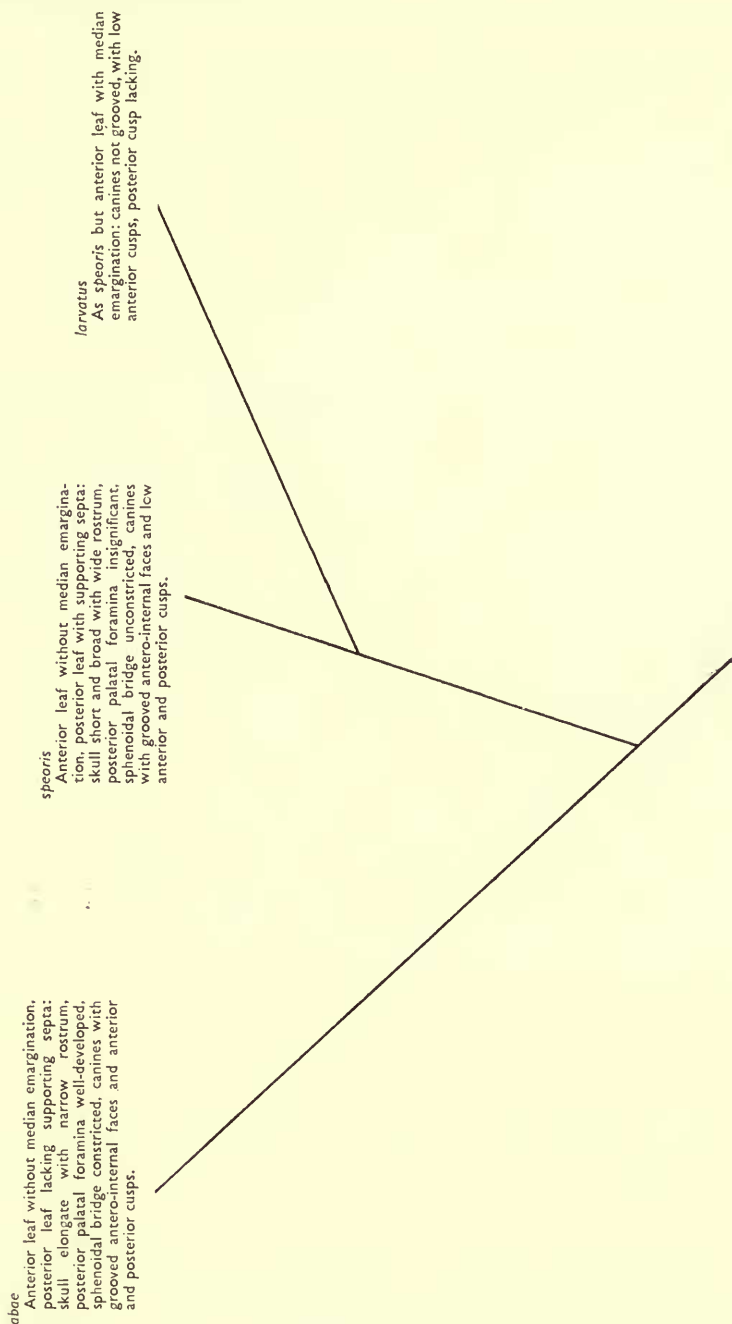


FIG. 30. Possible relationships in the *Hipposideros speoris* group

shaped or slightly U-shaped junction with the maxillae and partially or wholly enclose the anterior palatal foramina. The palate is short and wide with a V-shaped or U-shaped palation. The pterygoid wings are not greatly developed and the sphenoidal bridge is not widened, exposing elongate lateral apertures. There is a well-developed sphenoidal depression and the width of the cochleae is equal to their distance apart. The outer lobe of the upper incisors is obsolescent or absent and the upper canines have no definite cusps, although barely defined low anterior and posterior cusps are sometimes present. The anterior upper premolar (pm^2) is small and extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is obsolete or nearly obsolete. The outer lower incisors are greater in crown area than the inner pair and the anterior lower premolar (pm_2) is one half to two thirds the length and height of the second lower premolar (pm_4).

As presently defined, the *speoris* group includes three species, *H. abae*, *H. larvatus* and *H. speoris*. It is distributed in both the Ethiopian and Asiatic regions, with *H. abae* representing the group in Africa while *H. larvatus* and *H. speoris* are exclusively Asiatic in distribution. As might be expected, *H. abae* is rather sharply divided from the Asiatic species to much the same degree as the Ethiopian representatives of the *bicolor* group are from their Asiatic relatives, although its affinities lie nearer to the predominantly Indian species *H. speoris* than to the more Malaysian *H. larvatus*. The group is not one of extensive specialization in the manner of some of the members of the *bicolor* or *cyclops* groups and in fact the ears of its members retain some degree of antitragal modification and their nasal foliations are comparatively simple, apart from the development of a third lateral supplementary leaflet. The structure of the ears and noseleaves in the *speoris* group indicates quite clearly its affinity to the *bicolor* group, and similar indications are evident in its cranial architecture, although specialization has proceeded further. In the *speoris* group the anterior palatal foramina in *H. larvatus* are wholly enclosed within the premaxillae and in the other species partially so; the upper canine cusps are virtually obsolete and the crown area of the outer lower incisors is greater than the crown area of the inner pair. The *speoris* group apparently represents an offshoot of the line leading to the *diadema* group and has no close relation to the *pratti* and *armiger* groups, which represent a different line of modification characterized by the marked development of noseleaves, rostral region and mesopterygoidal region.

The species of the *speoris* group may be keyed :

- 1 Anterior leaf without median emargination : prominent supraorbital ridges, rostrum flattened, vomer not projecting beyond palate, upper canines with shallow antero-internal groove and low posterior cusp 2
- Anterior leaf with definite median emargination : supraorbital ridges barely developed, rostrum rounded, vomer projecting beyond palate, upper canines not grooved and lacking a posterior cusp *larvatus* (p. 98)
- 2 Posterior leaf with supporting septa : posterior palatal foramina undeveloped, palation U-shaped, sphenoidal bridge unconstricted *speoris* (p. 101)
- Posterior leaf lacking supporting septa : posterior palatal foramina prominent, palation nearly square, sphenoidal bridge constricted *abae* (p. 97)

Hipposideros abae J. A. Allen

Hipposideros abae J. A. Allen, 1917 : 432. Aba, Uele district, Congo.

The ears are very large, triangular and sharply pointed, with their posterior margins markedly concave behind the tip. There is no definite process at the antitragal lobe, but the ear membrane is thickened at this point. The anterior leaf has no median emargination and the internarial septum is not inflated, while the narial lappets are moderately developed. The intermediate part of the leaf is not greatly inflated and has a low median eminence flanked by weaker lateral eminences. The posterior leaf is thin and lacks supporting septa, with its upper edge semicircular and not lobate. The skull is slightly more elongate than the skull of *H. speoris*, with a low to moderate sagittal crest. The interorbital region is elongate and constricted with prominent supraorbital ridges. There is a very shallow frontal depression and the rostrum is narrow, with slightly inflated rostral eminences. The zygomata are slender anteriorly, with a high jugal process, and the anteorbital foramen is large and elongate, closed by a narrow bar. The premaxillae make a slightly wedge-shaped junction with the palate and partially or wholly enclose the elongate anterior palatal foramina. The posterior palatal foramina, small and insignificant in *H. larvatus* and *H. speoris*, are well developed and the palation is almost square. The mesopterygoid fossa is wide, with the vomer not projecting beyond the posterior edge of the palate and with expanded pterygoids. The sphenoidal bridge is narrow and sharply constricted, exposing large elongate lateral apertures. There is a well-developed sphenoidal depression and the cochleae are equal in width to their distance apart or are a little smaller. The upper incisors are large, weakly bilobed and situated near the outer corners of the premaxillae, while the upper canines have their anterior faces shallowly grooved and have a weak anterior cusp and a larger posterior cusp extending for one quarter of the height of the tooth. The anterior upper premolar (pm^2) is small, extruded, compressed between the canine and the second upper premolar (pm^4) with these teeth nearly in contact, while the posterior ridge of the third upper molar is one quarter or less the length of the anterior ridge. The crown area of the outer lower incisors is only slightly greater than that of the inner pair, and the anterior lower premolar (pm_2) is one half or slightly less the length and height of the second lower premolar (pm_4).

Hipposideros abae is divided sharply from *H. larvatus* and *H. speoris* by both external and cranial characters. It is a larger species, with the posterior leaf lacking supporting septa. Its interorbital region is more elongated than in the Asiatic species, its rostrum narrower with the anterior part of the maxillae bearing the canines more elongated, and it has a much larger anteorbital foramen. The premaxillae are broader and its prominent posterior palatal foramina, nearly square palation and constricted sphenoidal bridge are in direct contrast to the insignificant foramina, U-shaped palations and unconstricted sphenoidal bridges of *H. larvatus* and *H. speoris*. Such differences indicate comparatively remote divergence from the Asiatic members of the group and although in some respects such as its elongate skull and narrow, elongate rostrum *H. abae* is more primitive than *H. larvatus* or

H. speoris, it has the grooved upper canines of *H. speoris* and at the same time has developed independent specializations in its unsupported posterior leaf, prominent posterior palatal foramina and constricted sphenoidal region. The position of *H. abae* within the group is difficult to determine in view of these considerations. Its elongate skull and narrow rostrum suggest some affinity with the *bicolor* group and *H. abae* evidently forms a link between that group and the *speoris* group, but it is otherwise as specialized as *H. larvatus* and *H. speoris* in some features and in others perhaps more so. The degree of affinity of *H. abae* to its Asiatic relatives is similar to that of *H. jonesi* to its related Asiatic species in the *bicolor* group or to that of *H. cyclops* and *H. camerunensis* to the related Australian and Papuan species of the *cyclops* group. *Hipposideros abae*, however, is rather less divergent from its associated Asiatic species than *H. jonesi*, *H. cyclops* and *H. camerunensis* are from their closest congeners in the Asiatic and Australasian regions, perhaps reflecting a slightly less remote dichotomy in the *speoris* group. Its degree of divergence from its Asiatic relatives is paralleled by *H. caffer* and its associated species, which have a similar affinity to the Asiatic *H. galeritus* and its allies, while the African *H. commersoni* diverges less from the related Asiatic *H. diadema* than *H. abae* does from *H. larvatus* and *H. speoris*.

DISTRIBUTION : Portuguese Guinea (Veiga Ferreira (1949 : 192)) ; Guinea (Aellen (1956a : 888), Eisentraut & Knorr (1957 : 331)) ; Sierra Leone ; Ghana ; Nigeria ; Congo ; Uganda (first record : specimen from Metu, West Madi County, West Nile District, in collection of British Museum (Natural History)).

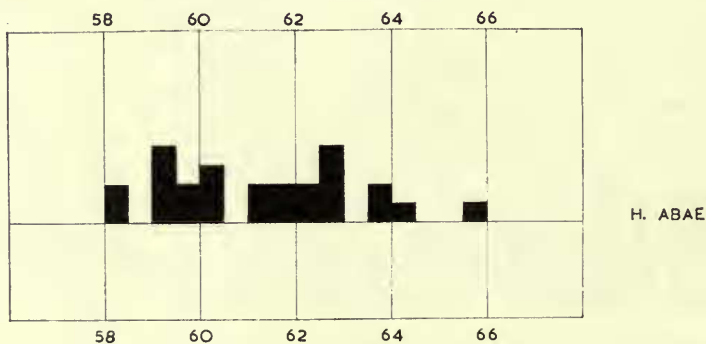


FIG. 31. Length of forearm in *Hipposideros abae*

Hipposideros larvatus

The ears are as described for the group, with a small process at the antitragal fold. The anterior leaf has a small but distinct median emargination, the inter-narial septum is uninflated and the narial lappets are well developed, the nostrils slightly pocketed. The intermediate part of the leaf is slightly expanded, with a moderate median eminence and weaker lateral eminences. The posterior leaf is moderate, supported by three well-defined septa, its upper edge semicircular but slightly flattened and thickened, displaying a tendency to become lobate. There is

a frontal sac in both sexes, in females reduced sometimes to a depression containing a tuft of hairs. The skull is short and massive, with a well-developed sagittal crest and low supraorbital ridges. There is a shallow frontal depression and the rostral eminences are well inflated, separated by a shallow groove, the rostrum rounded. The anteorbital foramen is slightly elongate. The premaxillae make an acutely V-shaped junction with the maxillae and wholly enclose the slightly elongate anterior palatal foramina. The palation is U-shaped, with the vomer projecting beyond the posterior edge of the palate and the sphenoidal bridge only very slightly constricted, nearly parallel-sided. The sphenoidal depression is well developed. The upper incisors are weakly bilobed, the upper canines with a low anterior cusp but no posterior cusp and with their antero-internal faces not grooved. The anterior upper premolar (pm^2) is slightly extruded and compressed tightly between the canine and the second upper premolar (pm^4), while the posterior ridge of the third upper molar is one quarter the length of the anterior ridge. The anterior lower premolar (pm_2) is one third to one half the length of the second lower premolar (pm_4).

Although *H. larvatus* is very similar to *H. speoris*, the two species are separated by a number of differences indicating comparatively recent divergence. Of the two, *H. larvatus* is perhaps slightly the more primitive, with a prominent median emargination in the anterior leaf, longer interorbital region with less prominent supraorbital ridges, longer, rounded rostrum and ungrooved canines, although these have lost the posterior cusp. The two species are more closely related to each other than either is to the African species *H. abae*, which displays some affinities to *H. speoris* but clearly is widely separated from the two Asiatic species. *Hipposideros larvatus* exhibits a cline in size in southeast Asia : *H. l. grandis* from Burma and *H. l. alongensis* from Indochina are the largest subspecies, while *H. l. barbensis* from St. Barbe Island and *H. l. larvatus* from Java are the smallest. Specimens from Siam approach *H. l. grandis*, while those from Sumatra and its adjacent islands are nearer in size to *H. l. larvatus* : *H. l. neglectus* from Borneo and the Malay Peninsula is intermediate between these extremes.

DISTRIBUTION : Burma to Indochina and the Malay Peninsula ; Java ; Borneo ; Sumatra and adjacent islands.

Hipposideros larvatus larvatus (Horsfield)

Rhinolophus larvatus Horsfield, 1823 : No. 6, pl. Java.

Rhinolophus vulgaris Horsfield, 1823 : No. 6, pl. Java.

Rhinolophus deformis Horsfield, 1823 : No. 6, pl. Java.

Rhinolophus insignis Horsfield, 1823 : No. 6, pl. Java.

DISTRIBUTION : Java.

Hipposideros larvatus sumbae Oei

Hipposideros larvatus sumbae Oei, 1960 : 28. Eastern part of Sumba Island, Lesser Sunda Islands. Lectotype designated by Bree (1961 : 122).

Hipposideros larvatus barbensis Miller

Hipposideros barbensis Miller, 1900 : 233. St. Barbe Island, South China Sea.

DISTRIBUTION : St. Barbe Island ; Johore Archipelago : Aor Island (Hill (1960 : 28)).

Hipposideros larvatus neglectus Sody

Hipposideros larvatus neglectus Sody, 1936 : 46. Roema Manoeal, south foot of Mount Kenepai, central Indonesian Borneo.

Miller (1942 : 116) refers a specimen from Nias Island to *H. l. neglectus* but suggests that it may prove separable from both *H. l. larvatus* and *H. l. neglectus* : Hill (1960 : 28) provisionally refers specimens from Butang Island and Simalur Island to *H. l. neglectus*.

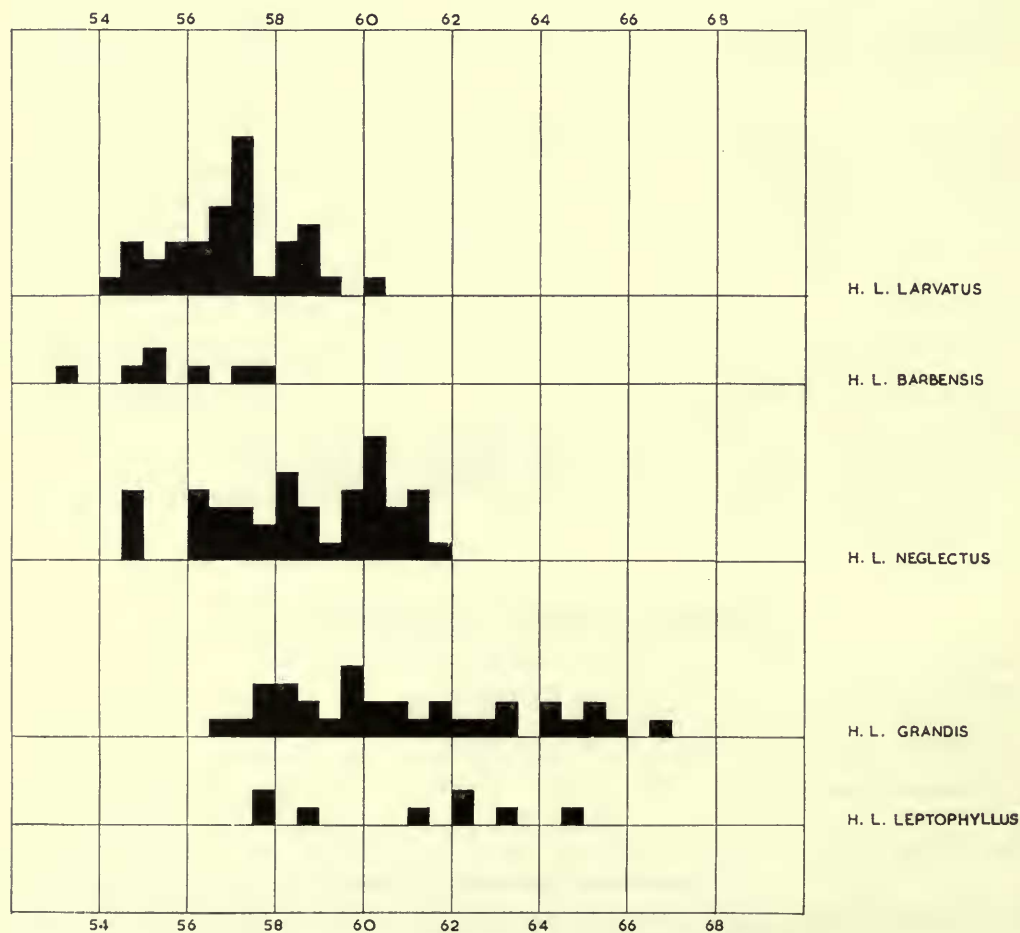


FIG. 32. Length of forearm in *Hipposideros larvatus*

DISTRIBUTION : Borneo ; Karimata Island ; South Natuna Islands : Sirhassen Island ; Sumatra ; Nias Island ; Simalur Island ; Butang Island ; Malay Peninsula ; Tioman Island.

***Hipposideros larvatus grandis* G. M. Allen**

Hipposideros larvatus grandis G. M. Allen, 1936 : 345. Akanti, Upper Chindwin, Burma, 500 feet.

Shamel (1942 : 322) compared *H. l. grandis* and *H. l. neglectus*.

DISTRIBUTION : Burma ; Siam (Shamel (1942 : 322)) ; Indochina (part).

***Hipposideros larvatus alongensis* Bourret**

Hipposideros larvatus alongensis Bourret, 1942a : 27. Bay d'Along, Indochina.

External measurements of a small series of specimens are given by Bourret (1942b : 10).

***Hipposideros larvatus poutensis* J. A. Allen**

Hipposideros poutensis J. A. Allen, 1906 : 483. Pouten, Hainan.

***Hipposideros larvatus leptophyllus* (Dobson)**

Phyllorhina leptophylla Dobson, 1874a : 234. Khasi Hills, Assam.

Hipposideros speoris

The ears are as described for the group, pointed, their posterior margins slightly concave behind the tip and have a small projecting process at the antitragal lobe. The anterior leaf has only a faint trace of a median emargination, the internarial septum is slightly inflated and the narial lappets are well developed, the nostrils slightly pocketed. The intermediate part of the leaf is slightly expanded, with inflated median and lateral eminences. The posterior leaf is supported by three septa and its upper edge is semicircular and not especially thickened. There is a frontal sac in male specimens : it is absent or represented by a tuft of hair in female examples. The skull is similar to the skull of *H. larvatus*, with a low to moderate sagittal crest and low but definite and more prominent supraorbital ridges. There is a shallow frontal depression and the rostral eminences are well inflated, the rostrum flattened dorsally. The premaxillae make an acutely angled wedge-shaped junction with the maxillae and partially or wholly enclose the rather elongate anterior palatal foramina. The palation is U-shaped and the vomer does not project beyond the edge of the palate. The sphenoidal bridge is moderate and only slightly constricted and there is a shallow but well-defined sphenoidal depression. The upper incisors are not bilobed or only very weakly so and the upper canines have low anterior and posterior cusps and a shallow groove on their antero-internal faces. The

anterior upper premolar (pm^2) is slightly extruded, compressed tightly between the canine and the second upper premolar (pm^4), while the posterior ridge of the third upper molar is one third the length of the anterior ridge. The anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4). Brosset (1962 : 608) provides a study of the biology of *H. speoris* in India, with measurements and notes on its colour variation.

DISTRIBUTION : India ; Ceylon.

Hipposideros speoris speoris (Schneider)

Vespertilio speoris Schneider, 1800 : pl. 59b. Tate (1941 : 377) has suggested restriction of the type locality to Tranquebar, India : it is briefly reviewed by Oey & Feen (1958 : 231).

Rhinolophus marsupialis Desmarest, 1820 : 126.

Rhinolophus dukhunensis Sykes, 1831 : 99. Deccan, India.

Hipposideros apiculatus Gray, 1838 : 492. Madras, India.

Hipposideros templetonii Kelaart, 1850a : 208. Ceylon.

Hipposideros aureus Kelaart, 1853 : 18. Ceylon.

Hipposideros blythi Kelaart, 1853 : 20. Ceylon.

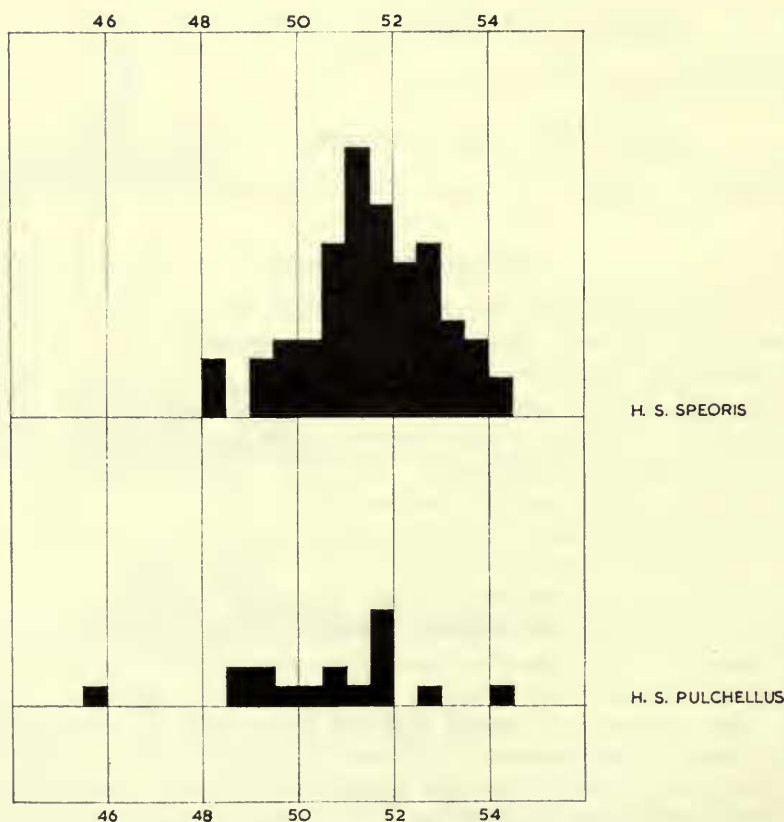


FIG. 33. Length of forearm in *Hipposideros speoris*

Oey & Feen (1958 : 227) discuss the date of description of *Vespertilio speoris* Schneider and reprint the original text. They also study (p. 232) the external differences between *H. speoris* and *H. larvatus* in considerable detail.

DISTRIBUTION : India (part) ; Ceylon.

Hipposideros speoris pulchellus Andersen

Hipposideros speoris pulchellus Andersen, 1918 : 383. Vijayanagar, Bellary, India.

DISTRIBUTION : India (part).

HIPPOSIDEROS DIADEMA group

The ears are triangular, acutely pointed, their posterior margins concave behind the tip, with no antitragal modifications. The noseleaf is comparatively simple, with three or four lateral supplementary leaflets. The anterior leaf has no median emargination and the internarial septum is not inflated. The intermediate part of the leaf is expanded and the posterior leaf is high, supported by a median septum and two weaker lateral septa. A frontal sac may be present or absent. The skull is large, with moderate or strongly developed cranial crests. A frontal depression is present in the majority of species. The rostral eminences are moderately inflated, the rostrum broad and high, its rounded upper surface level with the roof of the braincase. The zygomata are massive, with a prominent jugal process and the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a wedge-shaped junction with the maxillae and partially or wholly enclose the anterior palatal foramina. The palate is short, the vomer not projecting or projecting only very slightly beyond its posterior edge. The mesopterygoid fossa is wide, the pterygoid wings expanded, terminating in delicate processes. The sphenoidal bridge is wide, partially concealing elongate lateral apertures. The sphenoidal depression is moderately developed and the cochleae are large, their width as great or greater than their distance apart. The mandible is massive, with a deep symphysis and a high coronoid process : the angular process is sometimes flexed outwards. The upper incisors are bilobed, the upper canines with or without a posterior cusp. The anterior upper premolar (pm^2) is small, partially or wholly extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is much reduced and obsolescent. The crown area of the outer lower incisors is greater than that of the inner pair and the anterior lower premolar (pm^2) is from one third the length and height to one half or two thirds the length and height of the second lower premolar (pm^4).

As defined in the present paper, the *diadema* group has been extended to include the *commersoni* group as listed by Tate (1941 : 358), including solely the African species *H. commersoni*. There appears no good reason for the wide separation of this species from the *diadema* group since it shares with *H. diadema* and its associated species a number of features indicative of a common origin. Like *H. diadema* and its allies, it is characterized by its acute, triangular ears, simple noseleaf with

three or four lateral supplementary leaflets and massive skull with greatly developed cranial crests. As might be expected, the African *H. commersoni* is rather sharply

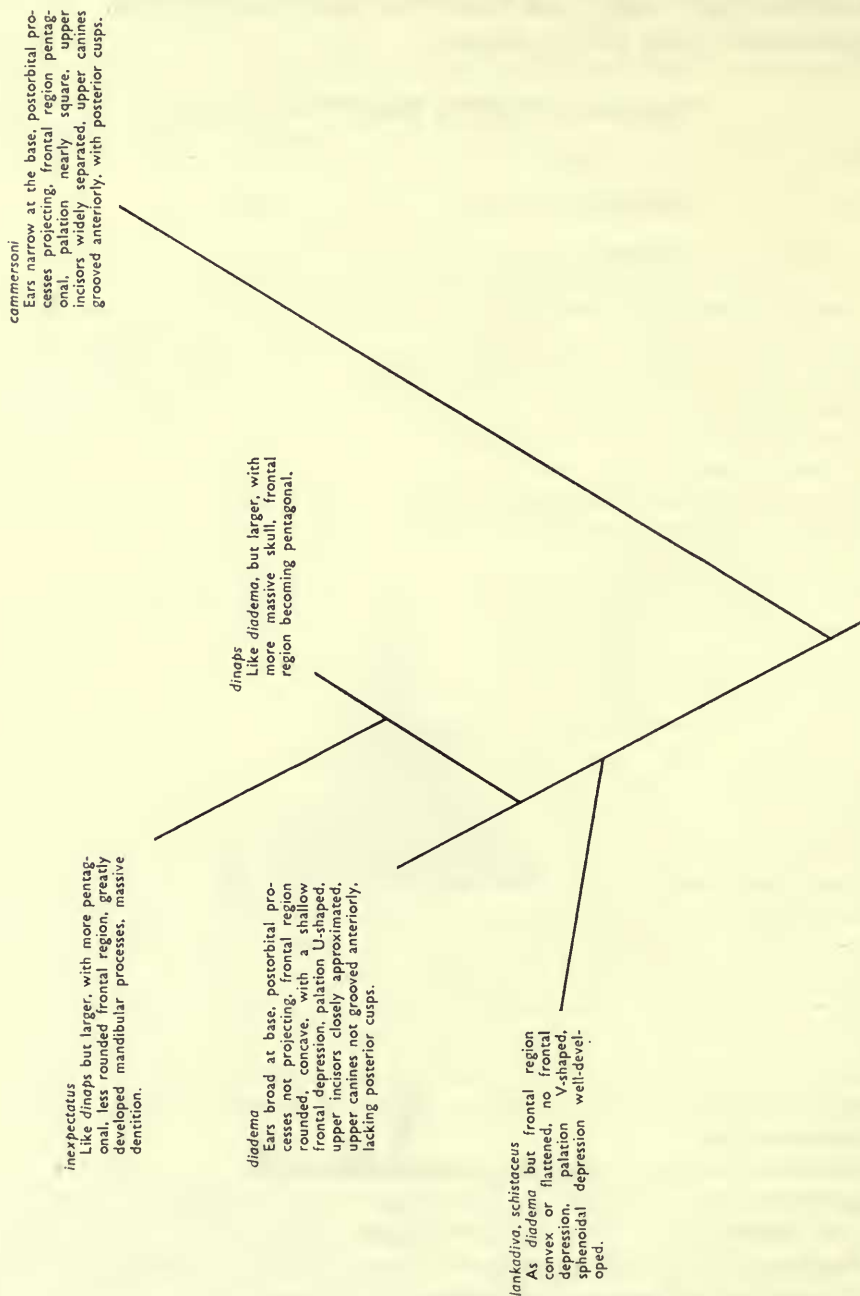


FIG. 34. Possible relationships in the *Hipposideros diadema* group

separated from *H. diadema*, which with its allies forms a comparatively closely related group of wholly Asiatic and Australasian species. In general, these are more primitive and less modified than *H. commersoni*, with broader ears, less developed postorbital processes, the naso-frontal region rounded from its dorsal aspect and not pentagonal, and with the upper canines not grooved anteriorly. *Hipposideros lankadiva* and *H. schistaceus* are the least specialized species in the group: *H. diadema* and more particularly its immediate derivatives *H. dinops* and *H. inexpectatus* are more modified, while *H. commersoni* is the most advanced species of the group, with narrow ears, projecting postorbital processes, more pentagonal naso-frontal region, grooved canines and with the anterior premolars (pm₂) more reduced. Possible relationships of the species of the *diadema* group are summarized in Figure 34.

The species of the *diadema* group may be keyed:

- 1 Ears broad at base: postorbital processes not projecting, naso-frontal region rounded, upper incisors in contact or nearly so, upper canines not grooved anteriorly, lacking posterior cusps 2
 Ears narrow at base: postorbital processes projecting, naso-frontal region pentagonal, upper incisors widely separated, upper canines grooved anteriorly, with high posterior cusp *commersoni* (p. 115)
- 2 Frontal region convex or flattened, no frontal depression; palation acute, V-shaped; sphenoidal depression well developed 3
 Frontal region concave, with a shallow frontal depression; palation rounded, U-shaped; sphenoidal depression shallow 4
- 3 Skull larger, condylocanine length exceeding 26.5 mm., length of maxillary tooththrow (c-m³) exceeding 12.0 mm. *lankadiva* (p. 105)
 Skull smaller, condylocanine length less than 25.5 mm., length of maxillary tooththrow (c-m³) less than 11.8 mm. *schistaceus* (p. 107)
- 4 Smaller, length of forearm less than 98.0 mm., condylocanine length less than 33.0 mm.; intermediate part of noseleaf with prominent median ridge, sometimes forming a projection 5
 Larger, length of forearm exceeding 100 mm., condylocanine length exceeding 34.0 mm.; intermediate part of noseleaf swollen but without a prominent median ridge or projection *inexpectatus* (p. 113)
- 5 Smaller, length of forearm less than 92.0 mm., condylocanine length less than 31.0 mm., length of maxillary tooththrow (c-m³) less than 13.8 mm. *diadema* (p. 108)
 Larger, length of forearm exceeding 92.0 mm., condylocanine length exceeding 32.0 mm., length of maxillary tooththrow (c-m³) exceeding 14.0 mm. *dinops* (p. 112)

Hipposideros lankadiva

The ears are large and acutely pointed, with their posterior margins slightly concave behind the tip. The noseleaf has usually four lateral supplementary leaflets, the fourth much reduced and rudimentary, sometimes absent. The anterior leaf has no median emargination and the internarial septum is not inflated, while the narial lappets are well developed. The intermediate part of the leaf is expanded, its central part inflated and swollen but not forming a distinct median ridge, flanked laterally by lesser eminences. The posterior leaf is high and broad, its upper margin semicircular, with a swollen median projection, flanked by narrow notches, and is supported by three well-defined septa enclosing small cells. The skull is large and

heavily built, with well-developed cranial crests. There is no frontal depression and the frontal region immediately anterior to the sagittal crest is convex or flattened. The zygomata are strong, with a high jugal process, while the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a U-shaped junction with the maxillae and enclose or nearly enclose the rounded anterior palatal foramina. The palation is V-shaped, the mesopterygoid fossa slightly narrowed with the vomer projecting slightly beyond the posterior edge of the palate. The sphenoidal bridge is wide, almost completely concealing elongate lateral apertures and the sphenoidal depression is well developed. The width of the cochleae is a little less than their distance apart. The mandible is massive, with a high coronoid process and the angular process flexed strongly outwards. The upper incisors are bilobed, the outer lobe a little larger than the inner lobe, and the upper canines are not grooved anteriorly : they have low anterior cusps but lack posterior cusps. The anterior upper premolar (pm^2) is small, extruded or partially extruded from the toothrow. The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is considerably greater than that of the inner pair, and the anterior lower premolar (pm_2) is one third the length and height of the second lower premolar (pm_4).

Hipposideros lankadiva is closely related to *H. diadema* but is perhaps slightly less specialized. Externally, it is very similar to *H. diadema*, but the intermediate part of the noseleaf has no definite median ridge and the median projection of the edge of the posterior leaf is more swollen and prominent. Cranially, it differs rather sharply in its convex or flattened frontal region, which lacks the frontal depression of *H. diadema*, in its V-shaped and not U-shaped palation and in its well-developed sphenoidal depression. With the very closely related *H. schistaceus* it represents *H. diadema* in the Indian subcontinent. Brosset (1962 : 621) has studied the biology of *H. lankadiva* in India and gives measurements and notes on its colour variation : this author suggests that in India the species is perhaps not subspecifically separable.

DISTRIBUTION : Ceylon ; Peninsular India.

***Hipposideros lankadiva lankadiva* Kelaart**

Hipposideros lankadiva Kelaart, 1850b : 216, Kandy, Ceylon.

DISTRIBUTION : Ceylon.

***Hipposideros lankadiva indus* Andersen**

Hipposideros indus Andersen, 1918 : 382. Gersoppa, Kanara, India.

***Hipposideros lankadiva mixtus* Andersen**

Hipposideros indus mixtus Andersen, 1918 : 382. Kolar, eastern Mysore, India.

The available material of this and the other subspecies of *H. lankadiva* is very limited, but there seems little difference between *H. l. indus* and *H. l. mixtus* and they are likely to prove synonymous.

***Hipposideros lankadiva unitus* Andersen**

Hipposideros indus unitus Andersen, 1918 : 382. Mundra, Saugor, Central Provinces, India, 1,600 feet.

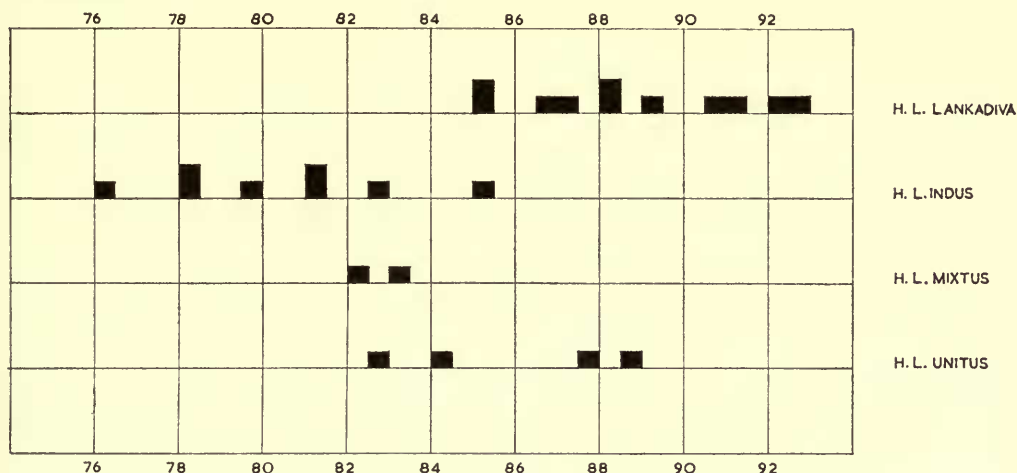


FIG. 35. Length of forearm in *Hipposideros lankadiva*

***Hipposideros schistaceus* Andersen**

Hipposideros schistaceus Andersen, 1918 : 382. Vijayanagar, Bellary, India.

Andersen gave only a brief diagnosis of this species. Its ears and noseleaf are exactly as in *H. lankadiva* but its coloration is paler and less brown and the skull, although resembling that of *H. lankadiva* very closely, is smaller, less massive, lower and flatter : the cranial crests are less developed and the cochleae are comparatively wider, their width equal to their distance apart. The remaining features of the skull, and its dentition, exactly resemble *H. lankadiva*. *Hipposideros schistaceus* is evidently very closely related to *H. lankadiva*, differing from this species chiefly in its smaller, less massive skull and relatively larger bullae. The

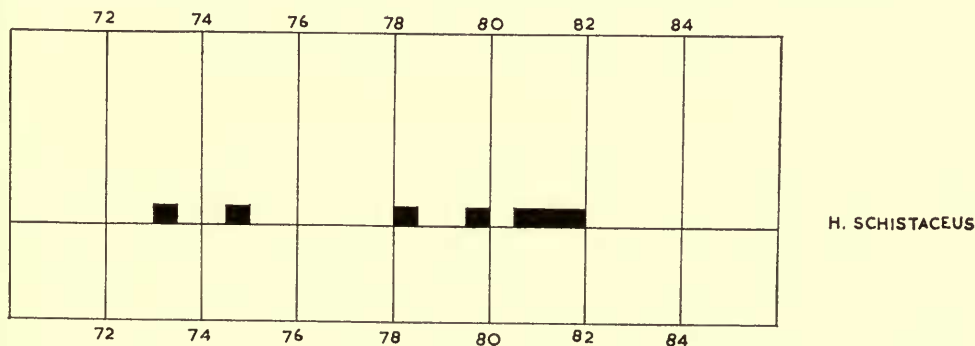


FIG. 36. Length of forearm in *Hipposideros schistaceus*

available material, both of *H. schistaceus* and of the smaller subspecies of *H. lankadiva*, is too limited to determine the extent of size variation in either *H. schistaceus* or *H. lankadiva*, and for the present their exact relationship must remain uncertain.

Hipposideros diadema

The ears are of moderate size, broad at the base and acutely pointed, with their posterior margins concave behind the tip. The noseleaf is well developed, with three or four lateral supplementary leaflets, the fourth small and sometimes rudimentary. The anterior leaf has no median emargination and the internarial septum is not inflated. The narial lappets are well developed and the nostrils are slightly pocketed. The intermediate part of the leaf is expanded with a prominent median ridge forming a median projection, flanked laterally by two much smaller projections. The posterior leaf is high, thick and fleshy, its upper edge semicircular, with a small median projection, and is supported by a median septum and two weak lateral septa. There is no frontal sac. The skull is large, its characters mainly those of the group. The cranial crests are moderately developed, the postorbital processes rounded and there is a shallow frontal depression. The rostral eminences are moderately inflated, the naso-frontal region from its dorsal aspect rounded and not pentagonal. The premaxillae make a wedge-shaped or slightly rounded junction with the maxillae and partially or wholly enclose the slightly elongate anterior palatal foramina. The palation is U-shaped or slightly V-shaped with the vomer projecting only very slightly beyond the posterior edge of the palate. The pterygoids and sphenoidal bridge are wide, almost completely concealing the elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are moderate, their width as great or nearly as great as their distance apart. The upper incisors are bilobed, the outer lobe usually a little larger than the inner lobe and are closely approximated with their tips convergent. The upper canines are not grooved anteriorly, and have no posterior cusps. The anterior upper premolar (pm^2) is small, partially or wholly extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is obsolescent or obsolete. The crown area of the outer lower incisors is considerably greater than that of the inner pair, while the anterior lower premolar (pm_2) is one half to two thirds the length and height of the second lower premolar (pm_4).

Hipposideros diadema has been divided into numerous subspecies over its extensive range, which includes almost the entire Indo-Australian region. As Tate (1941 : 373 et seq.) recognized, two broad groups of subspecies can be discerned among them. One group, composed of larger subspecies, is confined to the Asiatic mainland, Sumatra, Borneo, Java and their adjacent islands : the other, composed of smaller subspecies, is distributed from Celebes and the Philippine Islands eastwards to the Solomon Islands and northern Australia. There is some overlap between the two groups and larger subspecies are found in the Moluccas on the islands of Ceram and Batchian. Although in general the larger subspecies occur in the western parts

of the range of *H. diadema* and the smaller towards the eastern limits of its distribution, there appears to be little evidence of a clinal pattern of size variation.

DISTRIBUTION : Burma, Nicobar Islands and Philippine Islands east to the Solomon Islands and northern Australia.

***Hipposideros diadema diadema* (Geoffroy)**

Rhinolophus diadema Geoffroy, 1813 : 263, pls. 5, 6. Timor Island.

Rhinolophus nobilis Horsfield, 1823 : No. 6, pl. Java.

DISTRIBUTION : Timor Island ; Sumbawa Island ; Java.

***Hipposideros diadema masoni* (Dobson)**

Phyllorhina masoni Dobson, 1872 : 338. Moulmein, Burma.

Hipposideros diadema vicarius Andersen, 1905 : 499. Sarawak.

According to Andersen (1905 : 500) *Phyllorhina masoni* Dobson is of uncertain application but later (1907 : 6) he recognized it as a subspecies of *H. diadema* and gave brief diagnostic characters to separate this from the nominate subspecies. There appear to be no grounds for the separation of specimens from the Asiatic mainland from those of Borneo and Sumatra when large series are examined. Osgood (1932 : 221) gives notes on specimens from Annam and Shamel (1942 : 322) compares specimens from Siam with those from Java.

DISTRIBUTION : Burma ; Indochina : Annam (Osgood (1932 : 221)) ; Tonkin ; Siam (Shamel (1942 : 322)) ; Tenasserim ; Malay Peninsula ; Borneo ; Sumatra ; Nias Island (Miller (1942 : 117)).

***Hipposideros diadema nicobarensis* (Dobson)**

Phyllorhina nicobarensis Dobson, 1871 : 262. Nicobar Islands, Bay of Bengal.

***Hipposideros diadema enganus* Andersen**

Hipposideros diadema enganus Andersen, 1907 : 8. Engano Island.

Sody (1940 : 394) considers *H. d. enganus* to be a synonym of *H. d. masoni*.

***Hipposideros diadema natunensis* Chasen**

Hipposideros diadema natunensis Chasen, 1940 : 43. Bunguran Island, North Natuna Islands.

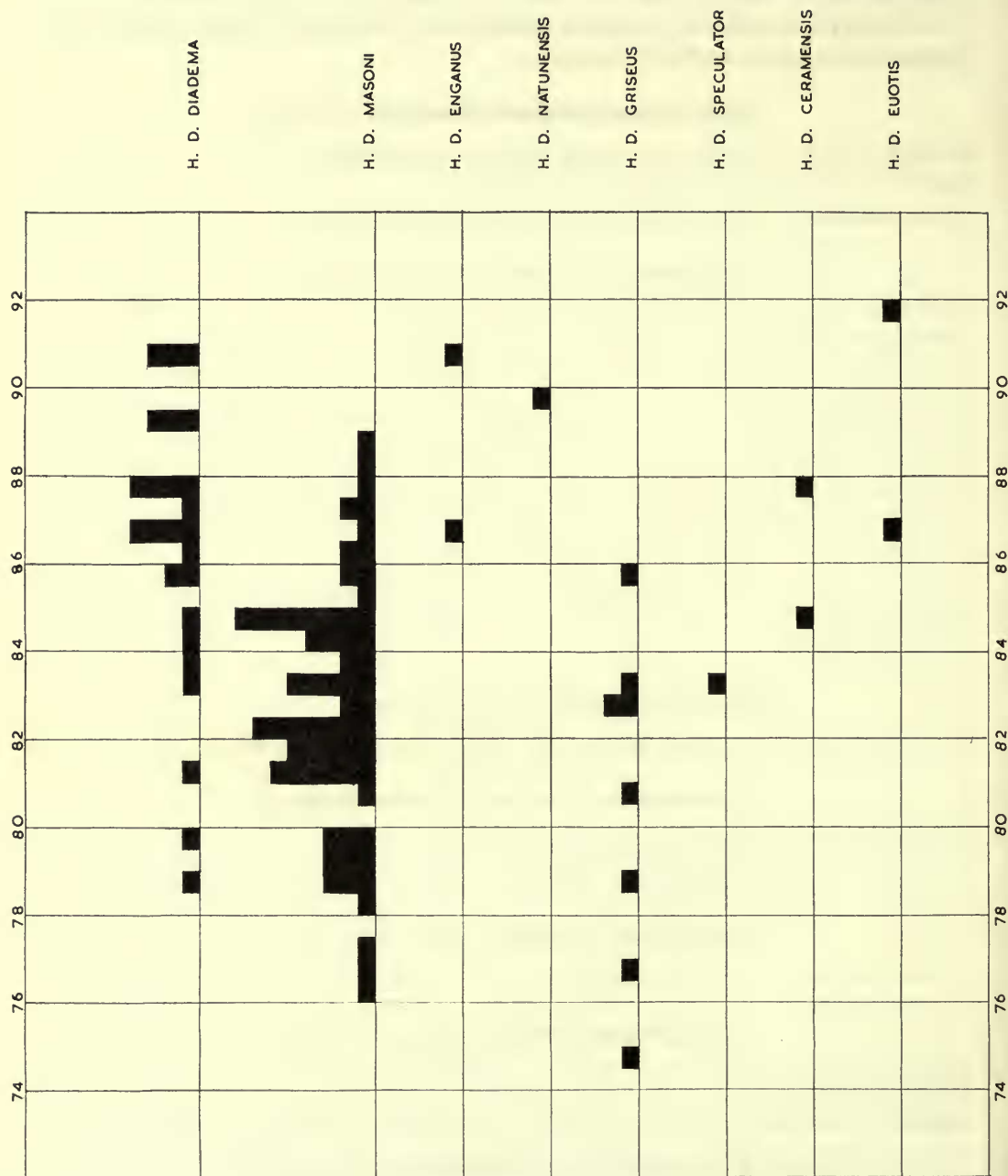
***Hipposideros diadema griseus* (Meyen)**

Rhinolophus griseus Meyen, 1833 : 608, pl. 46. San Matheo Cave, Montalban, near Manila, Luzon, Philippine Islands.

Hipposideros diadema anderseni Taylor, 1934 : 246. Novaliches, Rizal Province, Luzon.

Lawrence (1939 : 53) commented on the status of *H. d. anderseni*.

DISTRIBUTION : Philippine Islands : Mindoro ; Cebu ; Mindanao ; Catanduanes ; Leyte ; Luzon ; Guimaras.

FIG. 37. Length of forearm in *Hipposideros diadema*

Hipposideros diadema speculator Andersen

Hipposideros diadema speculator Andersen, 1918 : 381. Kalao Island, Flores Sea, south of Celebes.

DISTRIBUTION : Celebes ; Kalao Island.

Hipposideros diadema ceramensis Laurie & Hill

Hipposideros diadema ceramensis Laurie & Hill, 1954 : 58. Teleoti Bay, south Ceram Island, Molucca Islands.

DISTRIBUTION : Molucca Islands : Ceram ; Buru.

Hipposideros diadema euotis Andersen

Hipposideros euotis Andersen, 1905 : 502. Batchian Island, Molucca Islands.

Hipposideros diadema pullatus Andersen

Hipposideros diadema pullatus Andersen, 1905 : 498. Haveri, Papua, 700 metres.

DISTRIBUTION : New Guinea.

Hipposideros diadema custos Andersen

Hipposideros diadema custos Andersen, 1918 : 381. Ara, Kei Island.

Hipposideros diadema mirandus Thomas

Hipposideros demissus mirandus Thomas, 1914 : 437. Manus Island, Admiralty Islands.

Hipposideros diadema trobrius Troughton

Hipposideros diadema trobrius Troughton, 1937 : 276. Kiriwina Island, Trobriand Islands.

Hipposideros diadema oceanitis Andersen

Hipposideros diadema oceanitis Andersen, 1905 : 497. Guadalcanar, Solomon Islands.

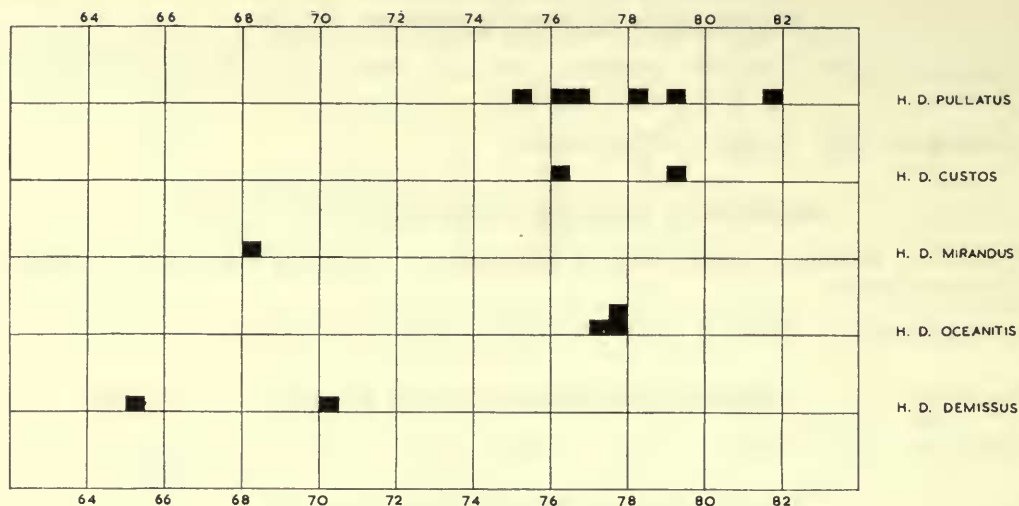
DISTRIBUTION : Solomon Islands : Guadalcanar ; Fauro ; Vella Lavella ; Ysabel ; Bougainville.

Hipposideros diadema demissus Andersen

Hipposideros demissus Andersen, 1909 : 268. Yanuta, San Christoval Island, east Solomon Islands.

Hipposideros diadema reginae Troughton

Hipposideros diadema reginae Troughton, 1937 : 275. Bloomfield River, Cooktown area, Queensland, Australia.

FIG. 38. Length of forearm in *Hipposideros diadema*

Hipposideros dinops

The ears are large, broad at the base and acutely pointed, their posterior margins concave just behind the tip. The noseleaf is large, with three lateral supplementary leaflets, the third small. The anterior leaf is broad and has no median emargination while the internarial septum is not inflated, the narial lappets are well developed and the nostrils slightly pocketed. The intermediate part of the leaf is expanded, with a prominent projecting median eminence, flanked laterally by much lesser swellings. The posterior leaf is thick and fleshy, its upper edge semicircular with a small, incipient median projection, and is supported by a median septum and two weak lateral septa. There is no frontal sac in the female type specimen. The skull is large, with well-developed lambdoid and sagittal crests. The postorbital processes are rounded and project very slightly, and there is a shallow frontal depression. The rostral eminences are moderately inflated and the rostrum is broadened, the naso-frontal region from its dorsal aspect very slightly less rounded and more angular than in *H. diadema*. The zygomata are moderate, with a prominent jugal process, and the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a V-shaped contact with the maxillae and do not enclose or only just enclose the elongate anterior palatal foramina. The palation is U-shaped, the vomer projecting only very slightly beyond the posterior edge of the palate. The mesopterygoid fossa is wide and the pterygoids expanded, with the wide sphenoidal bridge almost completely concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are a little wider than their distance apart. The mandible is massive, with a high coronoid process and with the massive angular process flexed slightly outwards. The upper incisors are strong and almost in contact, weakly bilobed, while the upper canines are massive and lack anterior or posterior cusps. The anterior upper premolar (pm²) is small and

extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact, while the posterior ridge of the third upper molar is almost obsolete. The crown area of the outer lower incisors is considerably greater than that of the inner pair and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4). *Hipposideros dinops* differs principally from *H. diadema* in its greater size, more greatly developed intermediate noseleaf, more angular naso-frontal region, more expanded zygomata and larger teeth. It is closely related to *H. diadema* and although evidently presenting some of the features of *H. diadema* in more exaggerated form, its angular, slightly pentagonal naso-frontal region, expanded zygomata and massive mandible are clearly correlations of the trend towards great size. In this respect, *H. dinops* links *H. diadema* to the giant species *H. inexpectatus* and displays to some extent the specializations of this species and of the more remotely related large African species *H. commersoni*.

DISTRIBUTION : Celebes ; Peleng Island ; Solomon Islands.

Hipposideros dinops dinops Andersen

Hipposideros dinops Andersen, 1905 : 502. Rubiana Island, Solomon Islands.

DISTRIBUTION : Solomon Islands : Rubiana ; Bougainville.

Hipposideros dinops pelingensis Shamel

Hipposideros pelingensis Shamel, 1940 : 353. Peleng Island, east of Celebes.

Hipposideros pelingensis Shamel is unrepresented in the collections of the British Museum (Natural History) but there seems very little doubt from its brief description that it is only subspecifically related to *H. dinops*. The tibia of *H. d. pelingensis* is shorter than that of *H. d. dinops* and Shamel says of the upper incisors that they "are small and bicusped, their inner cusps larger than the outer ones". In the type specimen of *H. d. dinops* the outer lobes of the upper incisors are slightly larger than the inner lobes. Tate (1941 : 374) referred a series from south Celebes to *H. d. pelingensis* and noted that in size they were almost as large as *H. d. dinops* from Rubiana Island. Apparently with reference to this series, Tate stated that the premaxillae do not wholly enclose the anterior palatal foramina : in the type specimen of *H. d. dinops* these apertures are just enclosed by the anterior enclosing processes of the premaxillae.

DISTRIBUTION : Peleng Island ; Celebes (Tate (1941 : 374, 387, 391)).

Hipposideros inexpectatus Laurie & Hill

Hipposideros inexpectatus Laurie & Hill, 1954 : 60. Posso (= Poso), north Celebes.

A very large species, with ears similar to those of *H. diadema*, very large and broad at the base, acutely pointed and with their posterior margins concave just behind the tip. The noseleaf is very large and has four lateral supplementary leaflets : the third leaflet is reduced and the fourth minute. The anterior leaf is

broad and has no median emargination. The internarial septum is not inflated and the narial lappets are well developed. The intermediate part of the leaf is greatly expanded with its central part much swollen and inflated but with only a very low, indefinite median ridge which does not extend to the upper margin of the intermediate part of the leaf : the swollen central part is flanked laterally by lesser eminences. The posterior leaf is thick and fleshy, its upper edge semicircular with a very small, incipient median projection and is supported by a narrow median septum and rather broader, less definite lateral septa. The skull is very large, with greatly developed lambdoid crests and an enormously developed, crescentic sagittal crest, merging into prominent supraorbital ridges. The postorbital processes project slightly and there is a shallow frontal depression. The rostral eminences are moderately inflated and the rostrum is broad, the naso-frontal region from its dorsal aspect slightly pentagonal, less rounded and more angular than in *H. diadema* or *H. dinops*. The zygomata are massive, greatly expanded and have a prominent jugal process, while the anteorbital foramen is very large and elongate, closed by a long, narrow bar. The premaxillae make a shallowly V-shaped junction with the maxillae and just enclose the slightly elongate anterior palatal foramina. The palation is U-shaped, the vomer projecting very slightly beyond the posterior edge of the palate, with wide mesopterygoid fossa, expanded pterygoids and large, wide sphenoidal bridge almost completely concealing elongate lateral apertures. There is a shallow sphenoidal depression and the width of the cochleae is a little greater than their distance apart. The mandible is massive, with a deep symphysis, high coronoid process and a thick, substantial angular process flexed strongly outwards. The upper incisors are large, their tips almost in contact and are weakly bilobed while the upper canines are massive and lack anterior or posterior cusps. The anterior upper premolar (pm^2) is small and extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact. The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is considerably greater than that of the inner pair, and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4).

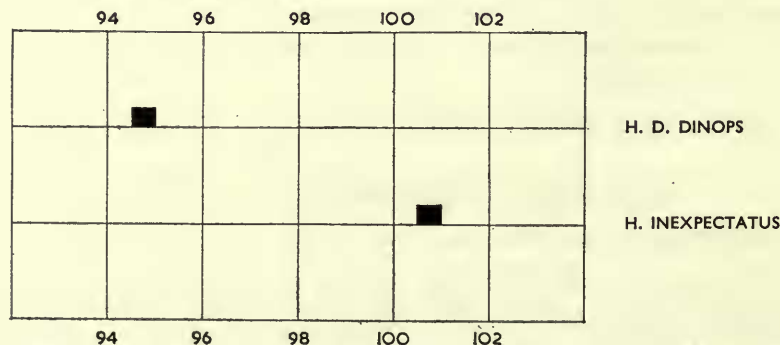


FIG. 39. Length of forearm in *Hipposideros dinops* and *H. inexpectatus*

Hipposideros inexpectatus is evidently closely related to *H. dinops*, but it differs from that species in its larger size, in its slightly less specialized intermediate nose-leaf, which has no definite median ridge or projection as in *H. dinops* and in the greater development of those cranial specializations associated with great size. The skull of *H. inexpectatus* is larger than that of *H. dinops*, with more greatly developed cranial crests, a more angular, slightly pentagonal naso-frontal region and a much more massive mandible, and in these features approaches the large African species *H. commersoni*. Its broad ears, closely approximated upper incisors and the absence of a groove in the anterior faces of the upper canines ally it indubitably to *H. diadema* and *H. inexpectatus* is evidently an extreme of the trend towards great size of which *H. dinops* is a part.

Hipposideros commersoni

A very large species with the ears narrow at the base, triangular, rounded at the tips and with their posterior margins concave just behind the tip. The noseleaf is large and not greatly specialized, with three or four lateral supplementary leaflets, the fourth small, sometimes rudimentary and rarely but on occasion absent. The anterior leaf is broad and has no median emargination and the internarial septum is not inflated, while the narial lappets are well developed and the nostrils are slightly pocketed. The intermediate part of the leaf is expanded, with a low, indefinite median ridge or eminence and lacking lateral inflations. The posterior leaf is of moderate height, its upper edge flattened, without a median thickening or projection, and is supported by a median septum and two very weak lateral septa. A frontal sac is present in both sexes, its opening more or less longitudinal. The skull is large, with well-developed lambdoid crests and a greatly developed sagittal crest merging into sharply defined supraorbital ridges. The postorbital processes project slightly and the rostral eminences are moderately inflated. The rostrum is broad and the naso-frontal region from its dorsal aspect is distinctly pentagonal in outline. The zygomata are strong with a prominent jugal process, and the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a V-shaped junction with the maxillae and wholly enclose the slightly elongate anterior palatal foramina. The palation is U-shaped, rather square, the vomer not projecting beyond the posterior edge of the palate. The mesopterygoid fossa is moderate and the pterygoids slightly constricted posteriorly, while the sphenoidal bridge is moderate, not excessively constricted, partially concealing elongate lateral apertures. There is a well-developed sphenoidal depression and the width of the cochleae is a little greater than their distance apart. The mandible is massive, with a deep symphysis, high coronoid process and a substantial angular process, flexed strongly outwards. The upper incisors are very weakly bilobed and set widely apart, at the outer margins of the premaxillae, while the upper canines have their anterior faces shallowly grooved and have low posterior cusps. The anterior upper premolar is very small, extruded from the toothrow, with the canine and the second upper premolar (pm⁴) in contact or nearly so. The posterior ridge of the third upper molar is obsolete or almost obsolete. The crown

area of the outer lower incisors is a little greater than that of the inner pair, while the anterior lower premolar (pm_2) is one half or less the length and height of the second lower premolar (pm_4).

Hipposideros commersoni stands rather sharply apart from the Asiatic species of the group by virtue of its narrower ears, pentagonal naso-frontal region, widely separated upper incisors and grooved upper canines, which possess low posterior cusps. Although in some respects *H. commersoni* is approached by the large Australasian species *H. dinops* and *H. inexpectatus*, these are basically species of the *diadema* type which appear to have developed specializations similar to those of *H. commersoni* as correlations of their large size, and *H. commersoni* must be regarded as a species of rather remote origin in the *diadema* group.

DISTRIBUTION : Madagascar ; eastern Africa south to Nyasaland and Northern Rhodesia ; Southwest Africa and Angola north to Gambia ; Congo.

***Hipposideros commersoni commersoni* (Geoffroy)**

Rhinolophus commersoni Geoffroy, 1813 : 263, pl. 5. Fort Dauphin, Madagascar.

DISTRIBUTION : Madagascar.

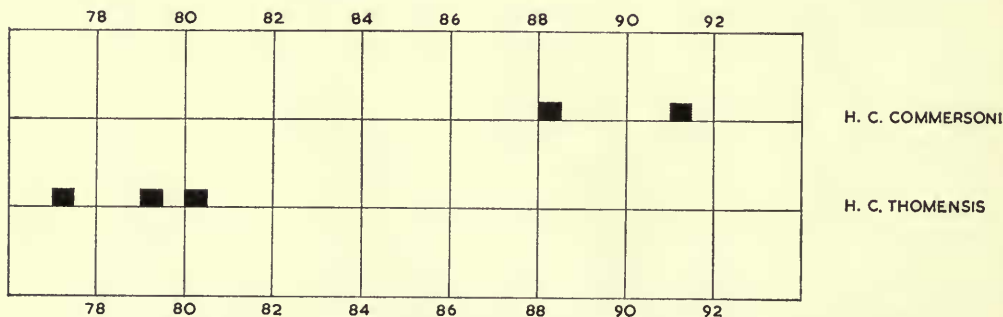


FIG. 40. Length of forearm in *Hipposideros commersoni*

***Hipposideros commersoni marungensis* (Noack)**

Phyllorhina commersoni var. *marungensis* Noack, 1887 : 272, pl. 10, figs. 31-33. Qua-Mpala, Marungu, western Tanganyika.

Hipposideros commersoni mostellum Thomas, 1904a : 385. Tana River, Kenya.

DISTRIBUTION : Kenya ; Tanganyika ; Zanzibar ; Nyasaland ; Northern Rhodesia ; Southwest Africa.

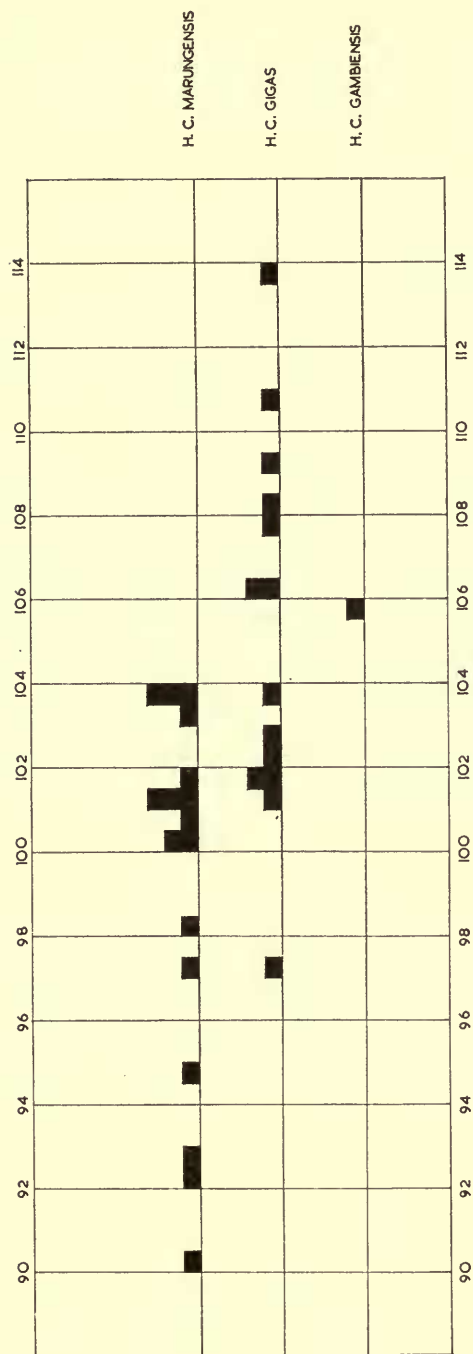
***Hipposideros commersoni gigas* (Wagner)**

Rhinolophus gigas Wagner, 1845 : 148. Benguela, Angola.

Phyllorhina vittata Peters, 1852 : 32, pl. 6, figs. 1-3, pl. 13, figs. 7-13. Ibo Island, Cap Delgado group, 12° 20' S. (in part, male co-type only : lectotype selected by Andersen (1906a : 45)).

(?) *Hipposideros gigas gambiensis* Andersen, 1906a : 42. Gambia.

Hipposideros gigas viegasi Monard, 1939 : 70. Madina Boé, Portuguese Guinea.

FIG. 41. Length of forearm in *Hipposideros commersoni*

Hipposideros gigas gambiensis was separated from *H. c. gigas* by Andersen on the grounds of slightly wider noseleaves. It seems unlikely to be a valid subspecies.

DISTRIBUTION : Angola ; Congo (part) ; Tanganyika (part) ; Cameroons ; Nigeria ; Ghana ; Guinea ; Portuguese Guinea ; Gambia.

***Hipposideros commersoni thomensis* (Bocage)**

Phyllorhina commersoni var. *thomensis* Bocage, 1891 : 88 and 1905 : 67. San Thomé Island.

***Hipposideros commersoni niangarae* J. A. Allen**

Hipposideros gigas niangarae J. A. Allen, 1917 : 438, pl. 51, fig. 1. Niangara, Uele district, Congo.

SUMMARY

The genus *Hipposideros* presents a wide range of morphological variation, and the characters of its numerous species rarely combine to indicate clearly defined natural groups or evolutionary trends. This revision, based chiefly on the features of the ears, noseleaf and skull, discusses the morphological criteria within the genus and its supraspecific groupings, recognizing seven species groups containing a total of forty-three species. These groups and their included species are described in some detail, with keys, and their probable relationships have been defined and discussed. These studies have suggested a less diffuse classification of *Hipposideros* than those proposed by earlier revisers, and indicate that despite the wide morphological dissimilarity of many of its species, the genus includes but three major evolutionary trends.

ACKNOWLEDGEMENTS

My thanks are due to Mr. H. M. van Deusen, Curator of the Archbold Collections of the American Museum of Natural History, who arranged the loan of specimens ; to Dr. G. B. Corbet, for his valuable suggestions on the presentation of data ; to Mr. R. W. Hayman, whose knowledge of Africa and of African bats has been readily available and to Miss Annette Bown, who prepared the illustrations and diagrams used in this paper.

TABLE 2—Summary of cranial measurements of *Hipposideros*

	Number of specimens	Condylacanthine length	Number of specimens	Rostral width	Number of specimens	Interorbital width	Number of specimens	Zygomatic width	Number of specimens	Mastoid width	Number of specimens	Length of maxillary toothrow (c-m ³)
<i>H. megalotis</i>	•	•	4	11·6–12·9 (12·3)	4	2·0–2·2 (2·1)	1	6·9	3	6·9–7·5 (7·1)	4	4·2–4·8 (4·5)
<i>H. bicolor pomona</i>	•	•	1	14·6	1	2·7	1	8·4	1	9·1	1	5·7
<i>H. bicolor genitilis</i>	•	•	25	14·5–15·9 (15·2)	34	2·4–2·9 (2·7)	24	8·3–9·0 (8·7)	26	8·7–9·3 (9·0)	34	5·8–6·2 (5·9)
<i>H. bicolor sinensis</i>	•	•	2	15·5–15·6	7	2·5–2·7 (2·5)	2	8·6–8·7	2	9·1–9·4	7	5·9–6·2 (6·0)
<i>H. bicolor atrox</i>	•	•	7	15·4–15·9 (15·6)	10	2·3–2·8 (2·5)	8	8·6–9·4 (9·2)	7	8·9–9·1 (9·0)	11	6·2–6·5 (6·3)
<i>H. bicolor major</i>	•	•	1	16·1	1	3·0	1	9·5	1	9·3	1	6·5
<i>H. ater ater</i>	•	•	18	13·2–13·9 (13·6)	26	2·1–2·5 (2·3)	21	7·9–8·3 (8·0)	21	8·1–8·5 (8·2)	26	5·1–5·5 (5·3)
<i>H. ater nicobarulae</i>	•	•	3	14·2–15·0 (14·6)	3	2·4–2·7 (2·5)	2	8·4–8·6	2	8·6–8·8	3	5·7–5·9 (5·8)
<i>H. ater saevus</i>	•	•	16	13·5–14·7 (14·1)	18	2·2–2·7 (2·5)	17	7·5–8·4 (8·0)	16	8·2–8·5 (8·3)	18	5·1–5·7 (5·5)
<i>H. ater anthricola</i>	•	•	2	13·7–14·7	2	2·3	1	8·3	2	8·2–8·4	2	5·3–5·8
<i>H. ater aruensis</i>	•	•	1	13·7	3	2·4–2·6	1	8·2	1	8·4	2	5·2–5·4
<i>H. ater gilberti</i>	•	•	2	13·5–13·9	2	2·0–2·2	2	7·9–8·2	2	8·2–8·4	2	5·3–5·4
<i>H. fulvus fulvus</i>	•	•	9	15·5–16·0 (15·8)	10	2·3–2·8 (2·6)	8	9·0–9·6 (9·3)	9	8·8–9·3 (9·1)	10	6·2–6·7 (6·4)
<i>H. fulvus pallidus</i>	•	•	17	15·0–16·4 (15·5)	21	2·2–2·7 (2·4)	21	8·6–9·6 (9·1)	18	8·6–9·1 (8·9)	21	6·0–6·8 (6·3)
<i>H. cineraceus cineraceus</i>	•	•	20	12·7–13·7 (13·2)	24	2·1–2·8 (2·5)	20	7·0–7·6 (7·3)	21	7·6–8·1 (7·8)	24	4·8–5·2 (5·0)

TABLE 2—Summary of cranial measurements of *Hipposideros* (Continued)

	Number of specimens	Condylacanthine length	Number of specimens	Rostral width	Number of specimens	Interorbital width	Number of specimens	Zygomatic width	Number of specimens	Mastoid width	Number of specimens	Length of maxillary toothrow (c-m ³)
<i>H. cinereus micropus</i>	1	12.6	1	3.5	1	2.5	1	—	1	8.0	1	4.9
<i>H. nequam</i>	1	—	1	5.2	8	3.4-3.8	8	10.7-11.6	7	—	1	6.3
<i>H. calcaratus</i>	5	19.0-19.5	8	5.1-5.2	8	(3.6)	8	(11.3)	7	9.7-10.5	8	7.9-8.4
		(19.2)		(5.2)		3.2-3.9		9.6-10.4		(10.1)		(8.2)
<i>H. cupidus</i>	1	16.7	2	4.4-5.0	2	3.2-3.9	2	9.6-10.4	2	9.5-10.0	2	7.2-7.3
<i>H. vidleyi</i>	1	17.1	1	5.9	1	3.0	1	9.4	1	10.6	1	6.6
<i>H. jonesi</i>	2	16.0-16.7	2	4.8-5.0	2	2.8-3.0	2	8.3-8.5	2	10.0-10.1	2	5.9-6.2
<i>H. dyacorum</i>	1	14.1	3	4.3-4.5	2	2.5-2.6	2	9.2-9.5	1	8.7	3	5.4-5.6
				(4.4)								(5.5)
<i>H. sabanus</i>	1	12.9	2	3.5-3.6	2	2.2-2.3	1	8.8	1	8.1	2	5.1
<i>H. obscurus</i>	1	—	1	4.9	1	2.5	1	9.4	1	9.2	1	6.6
<i>H. pygmaeus</i>	1	—	1	4.1	1	—	1	—	1	—	1	5.0
<i>H. galeritus galeritus</i>	2	15.7-15.8	5	4.5-5.2	4	2.7-2.9	2	9.7-10.1	3	9.0-9.2	5	6.3-6.6
				(4.9)		(2.8)				(9.1)		(6.5)
<i>H. galeritus brachyotus</i>	7	14.1-15.5	8	4.6-5.1	8	2.5-2.8	9	8.4-9.2	8	8.5-9.2	10	5.4-5.9
		(14.7)		(4.8)		(2.7)		(8.8)		(8.8)		(5.7)
<i>H. galeritus schneideri</i>	2	15.2-15.5	2	4.9-5.4	2	2.6-3.2	2	9.8-10.4	2	9.0-9.1	2	6.2-6.4
<i>H. galeritus labuanensis</i>	19	15.0-16.0	28	4.8-5.3	25	2.5-2.9	20	9.1-10.4	19	8.7-9.6	27	6.2-6.8
		(15.6)		(5.1)		(2.7)		(9.9)		(9.3)		(6.5)
<i>H. galeritus cervinus</i>	37	13.8-14.9	45	4.1-5.0	43	2.2-2.8	38	8.6-9.7	39	8.2-8.8	44	5.4-6.3
		(14.3)		(4.4)		(2.4)		(9.2)		(8.6)		(5.9)
<i>H. breviceps</i>	2	14.4	2	5.1-5.2	2	3.0	2	9.3-9.7	2	8.8	2	5.6-5.8
<i>H. curtus</i>	1	14.7	2	4.7-4.8	2	2.7-2.8	1	8.9	1	9.4	2	5.3-5.5
<i>H. fuliginosus</i>	2	20.3-20.5	3	5.9-6.4	3	3.3-3.7	2	12.0-12.9	2	11.5	3	8.0-8.6
				(6.1)		(3.5)						(8.3)

<i>H. caffer caffer</i>	.	.	73	14.0-15.2 (14.6)	92	4.1-4.7 (4.4)	86	2.3-3.2	76	8.6-9.5 (9.0)	83	8.8-9.5 (9.2)	87	5.4-6.2 (5.7)
<i>H. caffer tephrus</i>	.	.	8	14.1-14.5 (14.4)	8	4.1-4.3 (4.2)	7	2.6-2.8 (2.6)	7	8.5-8.9 (8.7)	8	8.7-9.1 (9.0)	8	5.5-5.8 (5.6)
<i>H. caffer ruber</i>	.	.	41	15.2-17.2 (15.9)	44	4.2-5.1 (4.5)	41	2.8-3.3 (3.0)	36	9.2-10.7 (9.9)	42	8.9-10.4 (9.8)	44	6.2-6.9 (6.4)
<i>H. caffer angolensis</i>	.	.	19	15.0-15.9 (15.5)	22	4.4-4.8 (4.6)	20	2.4-2.9 (2.7)	17	9.0-10.0 (9.3)	19	9.0-9.7 (9.4)	22	5.8-6.4 (6.2)
<i>H. caffer guineensis</i>	.	.	39	15.3-16.9 (15.8)	48	4.3-5.0 (4.8)	46	2.6-3.3 (3.0)	43	9.2-10.7 (10.2)	49	9.1-10.3 (9.8)	49	6.1-7.0 (6.7)
<i>H. beatus</i>	.	.	3	13.9-14.4 (14.0)	4	4.2-4.6 (4.4)	4	2.5-3.0 (2.8)	3	9.2-9.5 (9.4)	3	8.6-9.0 (8.8)	4	5.6-5.9 (5.7)
<i>H. cori</i>	.	.	1	16.9	1	5.9	1	3.3	1	9.3	1	10.2	1	6.4
<i>H. papua</i>	.	.	1	16.7	1	5.8	1	3.0	1	11.0	1	9.4	1	7.5
<i>H. cyclops</i>	.	.	26	23.0-26.2 (24.5)	27	7.9-8.8 (8.2)	27	2.7-3.6 (3.2)	25	14.3-16.1 (15.2)	27	11.3-12.6 (12.0)	27	9.7-10.8 (10.2)
<i>H. camerunensis</i>	.	.	2	25.9-27.1	2	9.6-9.7	2	3.4-3.7	2	16.3-16.4	2	12.9-13.2	2	9.8-11.1
<i>H. muscinus</i>	.	.	1	16.3	1	5.8	1	2.5	1	10.7	1	8.9	1	7.1
<i>H. wollastoni</i>	.	.	1	15.1	1	5.7	1	2.2	1	9.3	1	8.0	1	6.4
<i>H. senoni</i>	.	.	5	16.3-17.3 (16.8)	7	5.6-6.3 (6.0)	8	1.8-2.4 (2.0)	7	10.4-11.1 (10.8)	4	8.4-9.2 (8.7)	9	6.5-7.3 (6.9)
<i>H. stenotis</i>	.	.	.	—	1	5.1	1	2.1	.	—	1	7.8	1	5.6
<i>H. pratti</i>	.	.	2	27.7-27.9	2	10.5	2	4.5	2	16.9-17.5	2	15.3-15.5	2	11.9-12.0
<i>H. lylei</i>	.	.	15	24.9-25.9 (25.3)	15	9.3-10.0 (9.7)	15	3.9-4.8 (4.3)	12	14.5-16.0 (15.3)	14	13.0-14.2 (13.8)	15	10.5-11.3 (10.8)
<i>H. armiger armiger</i>	.	.	45	26.4-29.8 (28.0)	63	8.8-10.4 (9.6)	52	3.3-4.7 (4.1)	49	16.1-19.3 (17.6)	49	14.0-16.1 (14.9)	64	11.1-12.8 (12.1)
<i>H. turpis turpis</i>	.	.	3	23.0-23.1 (23.0)	8	7.4-7.8 (7.6)	8	3.3-3.6 (3.4)	3	14.1-14.5 (14.3)	3	12.9-13.1 (13.0)	8	9.7-10.2 (10.0)
<i>H. turpis pendleburyi</i>	.	.	1	23.6	1	7.9	1	3.8	1	15.0	1	13.1	1	10.1
<i>H. abae</i>	.	.	8	19.8-20.8 (20.4)	9	5.7-5.9 (5.8)	9	2.9-3.8 (3.4)	7	13.2-14.5 (13.7)	9	11.4-12.6 (11.9)	9	8.7-9.0 (8.9)
<i>H. larvatus larvatus</i>	.	.	17	18.5-19.8 (19.3)	21	5.9-6.4 (6.2)	19	2.9-3.2 (3.1)	18	11.7-12.8 (12.2)	18	10.5-10.9 (10.8)	21	8.1-8.7 (8.5)
<i>H. larvatus neglectus</i>	.	.	3	20.0-20.6 (20.2)	3	6.5-6.7 (6.7)	3	3.2-3.5 (3.4)	3	12.8-13.8 (13.2)	3	10.8-11.7 (11.3)	3	8.6-9.1 (8.8)
<i>H. larvatus grandis</i>	.	.	29	19.1-21.5 (20.4)	31	6.4-7.3 (6.9)	30	3.0-3.7 (3.3)	28	12.1-13.7 (13.1)	29	10.8-11.8 (11.3)	31	8.3-9.5 (8.9)

TABLE 2.—Summary of cranial measurements of *Hipposideros* (Continued)

	Number of specimens	Condylacanthine length	Number of specimens	Rostral width	Number of specimens	Interorbital width	Number of specimens	Zygomatic width	Number of specimens	Mastoid width	Number of specimens	Length of maxillary toothrow (c-m ³)
<i>H. larvatus leptophyllus</i>	8	20.9-21.4 (21.1)	8	7.4-7.7 (7.6)	8	2.8-3.3 (3.1)	8	13.4-14.0 (13.6)	8	11.6-12.2 (11.9)	8	8.9-9.4 (9.1)
<i>H. speoris speoris</i>	28	16.1-17.5 (16.8)	41	5.0-5.5 (5.2)	38	2.7-3.2 (2.9)	29	10.5-11.7 (11.0)	29	9.5-10.3 (9.9)	42	6.8-7.5 (7.1)
<i>H. speoris pulchellus</i>	18	15.8-17.3 (16.4)	17	5.0-5.4 (5.2)	18	2.6-3.2 (2.8)	18	10.1-11.1 (10.6)	18	9.3-10.4 (9.7)	18	6.7-7.2 (6.9)
<i>H. lankadiva lankadiva</i>	3	30.3-30.8 (30.6)	8	8.8-9.3 (9.1)	8	3.5-3.8 (3.7)	5	19.2-20.6 (19.8)	3	15.0-15.9 (15.5)	7	13.7-14.4 (14.0)
<i>H. lankadiva indus</i>	6	26.7-27.5 (27.2)	8	7.9-8.4 (8.1)	8	3.2-3.6 (3.4)	6	16.9-19.9 (17.8)	7	13.6-14.4 (14.2)	8	12.1-13.1 (12.6)
<i>H. lankadiva mixtus</i>	2	27.2-27.7	2	7.8-8.0	2	3.3-3.7	2	17.5-18.0	2	14.4	2	12.2-12.3
<i>H. lankadiva unius</i>	3	27.6-28.0 (27.9)	3	8.4-8.5 (8.5)	4	3.3-3.7 (3.5)	3	17.9-18.3 (18.1)	3	14.3-14.4 (14.4)	4	12.6-13.1 (12.9)
<i>H. schistaceus</i>	3	25.0-25.2 (25.1)	4	7.1-7.7 (7.4)	4	3.3-3.5 (3.5)	2	15.8-16.0	4	12.9-13.2 (13.1)	4	11.0-11.6 (11.3)
<i>H. diadema diadema</i>	12	27.1-30.0 (28.5)	16	8.8-9.7 (9.1)	15	3.3-4.1 (3.7)	11	17.0-19.6 (19.0)	12	14.0-15.5 (14.9)	16	11.8-13.5 (12.7)
<i>H. diadema masoni</i>	8	27.7-29.4 (28.4)	16	8.6-9.6 (9.1)	15	3.0-3.9 (3.6)	11	17.2-19.5 (18.4)	8	14.0-15.3 (14.7)	16	12.0-13.6 (12.6)
<i>H. diadema enganus</i>	1	29.2	1	9.9	1	3.6	1	—	—	—	2	13.1-13.8
<i>H. diadema natunensis</i>	1	28.6	1	9.8	1	3.9	1	18.6	1	14.6	1	13.3
<i>H. diadema griseus</i>	3	26.0-27.9 (26.8)	5	8.0-8.5 (8.3)	5	2.9-3.6 (3.4)	5	15.9-17.1 (16.5)	5	13.7-14.7 (14.3)	5	11.2-12.6 (11.8)
<i>H. diadema speculator</i>	2	27.2-27.6	2	9.1	2	3.8-4.0	2	16.8-17.6	2	14.3	2	11.9-12.2
<i>H. diadema ceramensis</i>	1	29.3	1	9.1	2	4.0-4.3	2	18.2-19.1	2	15.6-16.1	2	12.5-13.4

<i>H. diadema euotis</i> . . .	3	10.2-10.6 (10.4)	2	3.8-4.0	1	19.3	7	—	3	13.0-13.5 (13.3)
<i>H. diadema pullatus</i> . . .	6	26.0-27.5 (26.5)	8	3.1-3.7 (3.5)	6	16.9-17.8 (17.3)	7	14.0-14.7 (14.4)	8	11.3-12.1 (11.8)
<i>H. diadema custos</i> . . .	1	28.2	1	3.3	1	18.0	1	14.5	1	12.6
<i>H. diadema mirandus</i> . . .	1	24.8	2	3.2-3.3	2	15.1-15.4	2	13.3	2	10.7
<i>H. diadema oceanitis</i> . . .	2	26.6-27.1	3	3.5-3.6 (3.6)	3	16.9-17.7 (17.1)	3	14.0-14.1 (14.0)	3	11.0-11.7 (11.4)
<i>H. diadema demissus</i> . . .	2	—	2	3.2-3.4	2	14.7-15.2	—	—	2	10.2-10.9
<i>H. dinops dinops</i> . . .	1	32.5	1	3.6	1	20.7	1	16.5	1	14.2
<i>H. inexpectatus</i> . . .	1	34.7	1	3.7	1	22.4	1	18.4	1	15.2
<i>H. commersoni commersoni</i> . . .	2	27.1-27.6	4	2.8-3.4 (3.1)	3	15.2-16.8 (16.1)	3	13.8-14.0 (13.9)	4	10.1-11.0 (10.7)
<i>H. commersoni marungensis</i> . . .	14	28.5-31.8 (30.2)	15	3.1-4.0 (3.6)	15	17.4-19.9 (18.6)	15	14.5-18.0 (15.6)	15	11.5-12.6 (12.0)
<i>H. commersoni gigas</i> . . .	5	30.9-33.7 (32.2)	7	3.5-4.7 (3.8)	5	17.2-20.7 (19.5)	5	14.4-17.8 (16.3)	10	13.0-14.0 (13.5)
<i>H. commersoni thomensis</i> . . .	—	—	3	3.0-3.2 (3.1)	3	16.5-16.6 (16.5)	3	12.8-14.0 (13.4)	3	10.9-11.3 (11.0)

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